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Florence Signaigo Wagner 1919–2019

Photo credit: Michael J. Wynne

Florence Signaigo Wagner (2/18/1919 – 10/21/2019) was an integral member of one of the great teams in 20th century Botany, with her husband Warren H. (Herb) Wagner, Jr. Together, they revolutionized, in many ways, the way we look at and look for ferns. Her partnership with Herb, and her passing, at the age of 100, bookends a great flourishing of field studies of especially North American ferns.

Florence was born in Birmingham, Michigan, and spent much of her childhood in Michigan. The outdoors was always important as her father loved the land and always had what could perhaps be best described as a hobby farm, where the family would spend many weekends. Florence attended the College of William and Mary but graduated in 1941 with her BA in Philosophy with Distinction and Honors from the University of Michigan followed by her MA in Latin American Studies in 1943.

Even before they became life partners, Florence had already made her own contributions to botany. Her first interest in botany focused on red algae, with her doctoral work at the University of California, studying with the eminent phycologist George F. Papenfuss. She graduated in 1952, and published her

thesis as a major paper in 1954, where she described the new genus *Marionella*, named for her landlady, the renowned Berkeley embryologist and cytologist Marion S. Cave. While at Berkeley, she met and married (1948) fellow graduate student, Herb Wagner, and began a life partnership of pteridological adventure, moving back to Michigan when Herb joined the University of Michigan in 1951.

Florence brought rare gifts to the partnership. She anchored Herb's home life and, once the family was more independent, again took an active research role. Florence was a skilled cytologist at a time when knowledge of the role of chromosomes and the significance of chromosome numbers was expanding rapidly, with chromosome numbers being one of the cornerstones of biosystematics. She co-authored dozens of scientific papers with Herb and others, contributing extensive cytological data underpinning the conclusions. She also published a number of papers as sole or first author, especially on fern hybrids and fern chromosomes, and presented many papers and seminars, always with a keen sense of humor.

Later in her career – of course, Florence never retired – her interests were devoted to Ophioglossaceae, especially *Botrychium*, and the fern flora of Hawaii. *Botrychium* especially led Herb and Florence to many field trips throughout temperate and boreal North America, especially the northern Great Lakes region, the western mountains, and Alaska. The interest in Hawaii was Florence's last thrust, and she continued to work at the Herbarium on Hawaiian ferns until quite recently. Throughout her career, almost every new entity was named either as a team with Herb or by Herb himself, in joint papers, a notable exception being the Hawaiian filmy fern *Vandenboschia tubiflora* F. S.Wagner, Contr. Univ. Michigan Herb. 20: 243 (1995).

Florence held various research titles in Biology and the Herbarium at the University of Michigan, starting in 1961 as "Assistant in Research" later Research Associate, and from 1993 on, Research Scientist. She was unstintingly helpful to students, far beyond just the technicalities of cytology. She also was generous in devoting time and energy to professional societies. She held many offices in University, regional, and national societies. Most notably, she served as Chair of the Pteridological Section of the Botanical Society of America (1982-1984) and as Vice-President (1984-1985) and President (1986-1987) of the American Fern Society.—A.A. REZNICEK, University of Michigan Herbarium, Ann Arbor MI 48108

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Mothers of Pteridology

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Abstract.—Women have long been underrepresented in STEM, although there are certain fields within this umbrella that show less of a disparity — the biological sciences being one example. Within biology, pteridology has a rich history of female contributors involved since its inception. In this review we strive to highlight some of the foremost female pteridologists including Elizabeth Knight Britton, Alma Stokey, Irene Manton, Alice Tryon, Barbara Hoshizaki, and Florence Wagner. This is not an exhaustive list, but rather an insight into the strong maternal lineage of the fern and lycophyte community. While the field would not be the same without the work of many male pteridologists, herein we emphasize the important contributions that these founding women have made. Some of the research conducted by early female pteridologists was largely undermined by their time and circumstance; here we bring their lives and works to the foreground. Furthermore, we hope this paper inspires young botanists to enter our unique and historically rich field.

Key Words.—historical women, ferns, pteridology, women in science, history of science

> "My pine lot is truly a fern-land, as I discovered to my surprise not long ago when my eyes were opened and I became a fern lover... When the list in my pine lot had reached sixteen, I climbed my neighbor's fences and wandered farther afield."
> — Edith Scamman, 1923

Introduction

In 1893 *The Linnean Fern Bulletin*–later becoming the *American Fern Society*–unfurled as a small chapter of the *Agassiz Association for the Study of Nature* (Clute, 1902; Winslow 1919; Clute, 1943). The founding members of the society included Mr. Willard N. Clute, Mr. Henry C. Cowles, Mrs. T. D. Dershimer, Mr. Reuben M. Strong, Mr. James A. Graves, and Mrs. A. D. Dean, with the goal to "promote the study of ferns by correspondence, the exchange of specimens, the publication of knowledge thus obtained, [and] the promotion of field trips for ferns," (Clute, 1943). Pteridology was starting to grow, and the initiation of a centralized society helped amalgamate the field. Since its inception, the society had a strong female presence. Mrs. T. D. Dershimer helped initiate the society, was the first secretary, and later became the second elected Vice President in 1894 (Clute, 1894). Many female authors were

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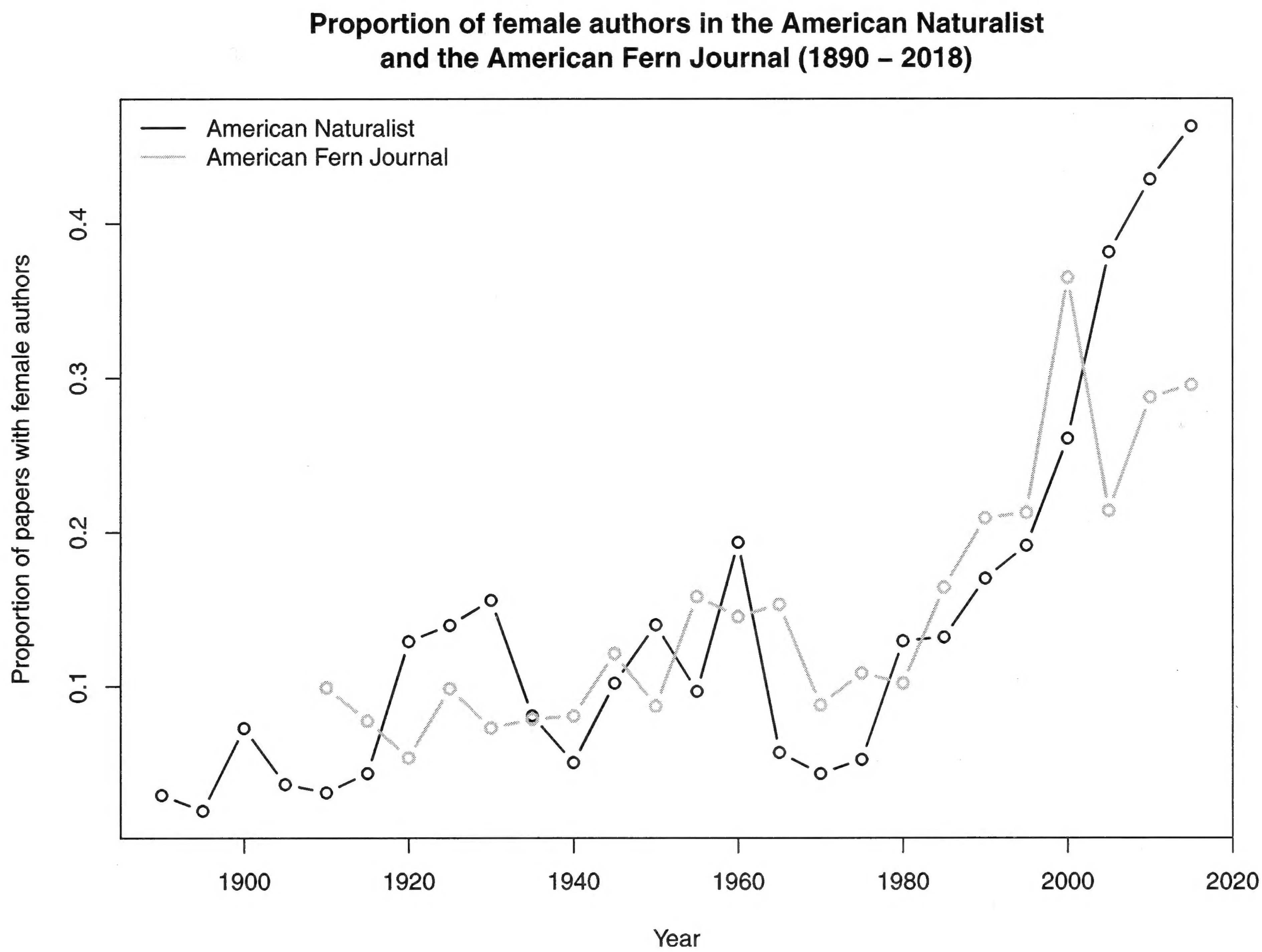

FIG. 1. Proportion of papers with female authors from the American Fern Journal (light gray line) of papers (collected by SPK), and proportion of papers with female authors from the American Naturalist (black line; data from Bronstein & Bolnick, 2018), measured in cumulative 5-year increments.

included in the first volume of the journal, such as Nellie Mirick (Vol. 1 No. 1), Kate D. Spalding (Vol. 1 No. 3), Elizabeth G. Britton (Vol. 1 No. 4), and Emily H. Terry (Vol. 1 No. 6). The prevalence of women early in the history of a scientific society was uncommon, but not restricted to pteridology.

Other journals in the biological sciences also have a long history of female involvement. Recently, Bronstein and Bolnick (2018) published an article in *The American Naturalist* (*Am. Nat.*), reviewing female authorship in the journal since its beginnings in 1867 (Fig. 1). They found that from 1867 to 1970, the proportion of female authorship was variable, ranging from around 0.03 to 0.2. Since the 1970s, however, there has been a steady increase in the number of female authors publishing in the *Am. Nat.* with nearly half of all papers in the journal having at least one female author today (Bronstein and Bolnick, 2018). We found a similar pattern in *The American Fern Journal* (*AFJ*) (Fig. 1), with the proportion of female authorship being relatively low from 1910 to 1970, however the *AFJ* had slightly less variability than the *Am. Nat.* in female authorship through this time period. Since the 1970s, female authorship in the *AFJ* has increased consistently as well. A notable difference is that the proportion of female authors in the *Am. Nat.* is nearly twice that of

the *AFJ* today. It will be intriguing to see how the number of female authors in the *AFJ*, and other biology-centered journals, changes in years to come. We hope to see a further increase in female contributions to the *AFJ*, and hope this review will inspire young female pteridologists to pursue a career in our field.

Historical Women in Pteridology: Premise

The field of pteridology had a strong base of foundational women early in its history. Both directly or indirectly, these pioneering women have influenced our field and the people within it. In addition, the diversity of male and female contributions has been important for the growth and development of the field. In the following pages, we highlight some founding mothers of pteridology. This is not an exhaustive list, but rather an insight into the strong maternal lineage of the fern community. Additionally, as some of these pteridologists' work was undermined by their time and circumstance, we wish to bring their lives and works to the foreground.

These women, as exemplified by the opening quote from Edith Scamman (Scamman, 1923), were unconditional lovers of not just ferns, but of the natural world and scientific exploration. Their enthusiasm and ingenuity contributed to some of the most important pteridological discoveries to date, while it also nurtured and inspired subsequent works by women and men alike.

Historical Women in Pteridology: Biographies

Margaretta Riley (1804–1899).—Margaretta "Meta" Riley is regarded as the first female pteridologist, having contributed much to the field in its earliest days. She was born in 1804 in Nottingham, England to Richard and Margaretta Hooper. Meta's father worked in the hosier and cotton business, and the family was fairly well-off (Creese, 2000). Meta Hooper married John Riley in 1826 and moved to the nearby village of Papplewick. The couple shared a passion for the collection, cultivation, and classification of ferns, and would go on to contribute greatly to the understanding of the British fern flora (Ellis, 2004).

Although Meta worked closely with her husband, she was not always credited as an author on their final works, so her full contribution to pteridology is unknown (Ellis, 2004). Despite this, records do show that Meta made several advancements in the growing field. During the late 1830s, she donated a complete pressed collection of Britain's fern flora to the Botanical Society of London. She also published on the classification of *Cystopteris* and *Thelypteris* in England, and, along with her husband John, published a comprehensive review of the cultivation of native English ferns (Allen, 1978). In 1838, John Riley was elected to the Botanical Society of London, following a paper on fern hybridization; Meta was elected to join the following year, an unusual honor for women at the time (Ellis, 2004; Allen, 1978).

Meta's contributions to the botanical world ended after John's death in 1846 (Creese, 2000). After his passing, she donated their extensive collection of

dried and living specimens to other botanists and museums, but remained a member of the Botanical Society of London. In lieu of botany, Meta took up interest in gardening, watercolor painting, poetry, history, philosophy, and politics. She died of bronchitis in 1899 at the age of 95 (Ellis, 2004). Her name and impact persist in broader venues than pteridology, as a large crater on Venus was named after her in the late 20th century: The Riley Crater (NASA/JPL, 1996).

Sarah "Sadie" Frances Price (1849–1903).—One of Kentucky's most well regarded botanists of the 19th century was the amateur naturalist Sarah "Sadie" Price. Sadie, the daughter of Maria and Alexander Price, was born in Evansville, Indiana. The family moved to Bowling Green, Kentucky when Sadie was a young child; it was here that she spent 12 years with her older brother Frederick and sister Mary. The beginning of the Civil War in 1861 proved difficult for the Price family; soon after the war began, Frederick was enlisted in the Union and the rest of the family left their work and moved back to Indiana (Lovell, 1959). During this time Sadie was educated at St. Agnes Hall. In the following decade both Sadie's brother and her parents passed away in 1873 and 1875, respectively. At the age of 26, Price was bedridden with unexplained back pain, but her passion for the natural world trumped her mortal woes and despite her ailments she would teach art courses in watercolor painting. Her students would bring plants and other wildlife to her bedside as items for illustration (Green and Rollins, 2005). After traveling to visit physicians in Philadelphia to treat her back pains, she was healthy and botanizing by 1880.

Following her return to good health, Price began a vigorous career in natural history. On top of thousands of botanical illustrations, she published 24 botanical manuscripts, and 40 scientific papers (Green and Rollins, 2005), including works on the ferns of Kentucky, rare species of *Asplenium,* and on cave ferns (Price, 1893; 1901; 1904). In 1897 Sadie published *The Fern-Collector's Handbook and Herbarium*, an 80-page treatise on ferns of the northern United States including detailed descriptions of over 70 species. As a skilled artist, Sadie provided detailed illustrations for each species in the handbook and her attention to detail can be captured in these lovely illustrations (Fig. 2A and 2B). Additionally, she included figures on the putative characters that unite some of the common species in the northern U.S., which is a boon to any flora. On top of illustrations and keys, in the preface of her handbook Ms. Price included descriptions of how to properly preserve and mount herbarium specimens for the layperson.

While Sadie was the premier botanist of Kentucky and impactful in early pteridology, her work and contributions may have been broadly overlooked because of John Williamson's *Flora of Kentucky*, published two decades prior (1878). The Flora of Kentucky was the first state fern flora in the United States which, in retrospect, seemed to overshadow subsequent work in the state. While his work was foundational, Sadie nonetheless expanded on it to include ferns of the broader northern United States (Price, 1901). She also corrected

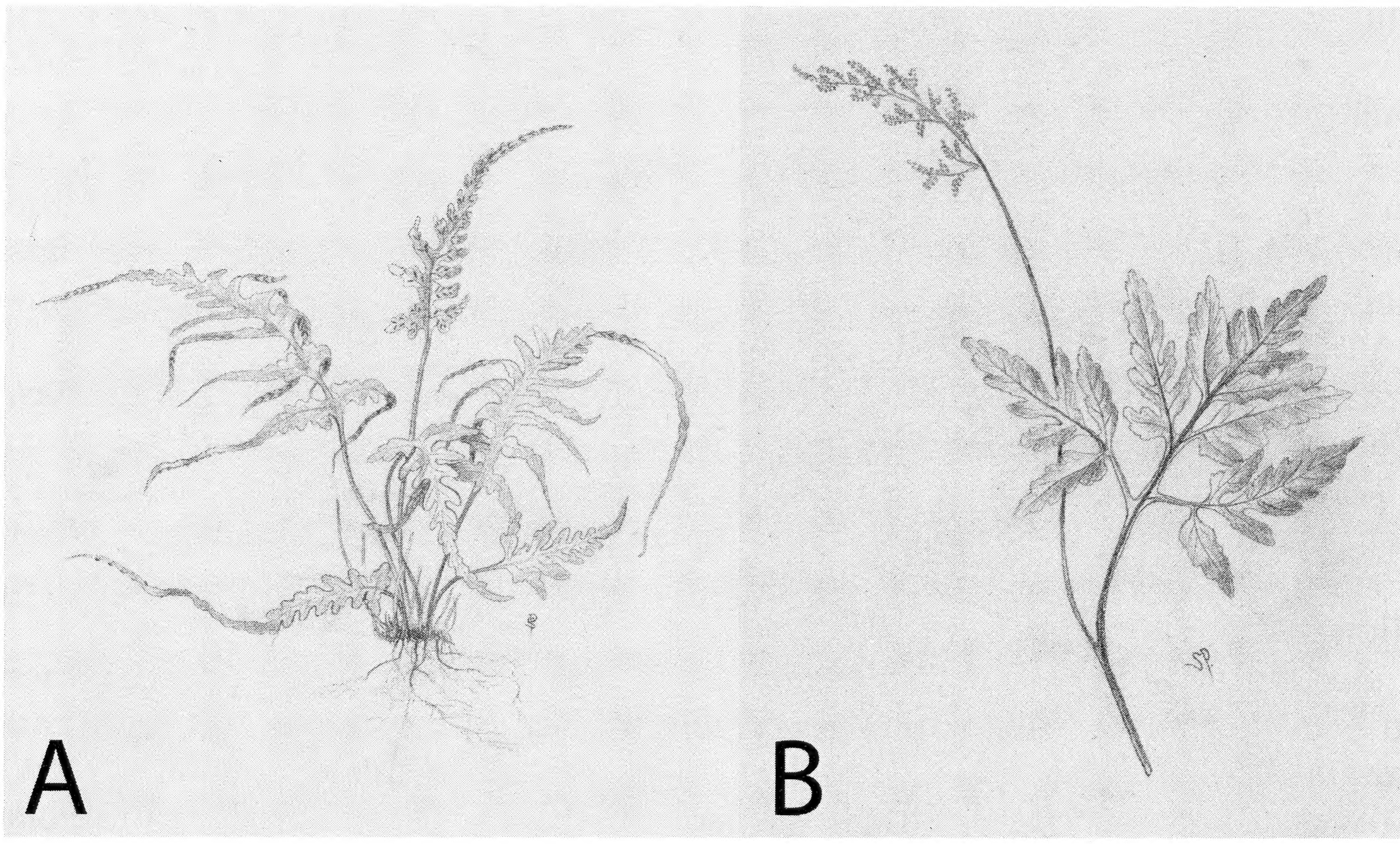

FIG. 2. Sadie Price illustrations of A. *Asplenium pinnatifidum*. B. *Botrychium virginianum*. Photo credit: Missouri Botanical Garden Archives.

some of Williamson's work, specifically on the genus *Ophioglossum* and its prevalence in North America (Price, 1897).

Not only did Ms. Price directly work and publish on ferns, but her enthusiasm for these organisms is expressed throughout her other publications. She advocated for the conservation of ferns; she was greatly concerned about some of the more "beautiful forms" and how they were being destroyed in the eastern mountains (Lovell, 1959). Sadie's work was a boon to the study of ferns in Kentucky during a depauperate period of pteridology in the state. The significance of her work was not only appreciated by practicing botanists, but also by lay plant lovers. In a review of Sadie's fern handbook published in the *Fern Bulletin* (v. 5 page 36), it was said that her "volume [is] designed to assist the beginner in fern study… one who knows nothing about botany, may identify any fern in the region mentioned, by merely turning the pages until [they] come to the illustration that matches the specimen." This review is not only an ode to her artistic abilities, but to her desire to engage lay folk in the study and appreciation of ferns.

In addition to her publications, Sadie's contributions include 2,912 herbarium sheets as well as about 965 watercolor illustrations (Green and Rollins, 2005). In 1903, Sadie passed away relatively young at the age of 54. She left behind many works still unpublished, some of which were picked up and published posthumously by her sister Mary Price (Lovell, 1951; 1959). Mary sold Sadie's herbarium specimens to the Missouri Botanical Garden where they are now housed. In one of her several obituaries, Reverend Frank Thomas regarded her as "a true high-priestess of nature," (Green and Rollins,

2005); she had a strong influence on the botanical community, and her work lives on through her thousands of botanical illustrations and important publications.

Elizabeth Gertrude Knight Britton (1858–1934).—Elizabeth Knight was born in New York City on January 9th, 1858 (Fig. 3). As is true with many of the pioneering women in pteridology, Ms. Britton did not receive a graduate degree and never held a formal salaried job. Despite these setbacks she published over 340 manuscripts and was a figurehead in the botanical community (Barnhart, 1935). She spent much of her early life in Matanzas, Cuba where her grandfather owned a sugar plantation and factory (Barnhart, 1935). This time was spent with her sisters and father naturalizing the island's ecosystem; these experiences must have been strongly influential in her botanical interests as she continued the study of natural history throughout her life.

As Elizabeth grew older, she spent much of her time with her grandmother in New York where she attended private school. She went on to enroll and graduate from Normal (now Hunter) College in 1875 at the age of 17. In 1885, Elizabeth married Nathaniel Britton who worked as a geologist at Columbia University. Nathaniel was interested in plants, but fully transitioned to studying botany following his marriage to Elizabeth (Creese, 2000). Elizabeth was a vivacious individual whose personality was infections. Her overall accomplishments in botany landed her a spot as one of the *American Men of Science,* now aptly *American Men and Women of Science* (Creese, 2000). While she was primarily known for being a figurehead in bryology, she had a passion for ferns and published on them throughout her career.

She contributed to pteridology in her treatment of Ophioglossaceae (Britton, 1897), Schizaeaceae (Britton, 1901; Britton and Taylor, 1901), Hymenophyllaceae (Britton, 1902), and Pteridaceae (Britton and Taylor, 1902). One of her most significant findings in pteridology was her documentation of the relationship between fungal hyphae and *Schizaea* gametophytes (Britton and Taylor, 1901). She noted that the fungus forms a symbiosis with the gametophyte and then with the developing sporophyte. This was an interesting finding at the time because mycorrhizal association with *Schizaea* gametophytes had not yet been observed. Elizabeth made significant contributions to pteridology in its early days; she was influential in many ways from her publications to her philanthropy.

In total she published 16 papers on ferns including an account of one of the only collected individuals of *Schizaea pusilla* in Nova Scotia, this specimen was sent to Asa Gray of Harvard University (Britton, 1896; Howe, 1934). She continued with her fern studies publishing revisions of North American *Ophioglossum* (Britton, 1897), and capped it off with final expeditions to Cuba (Britton, 1911) and Bombay (Britton, 1923).

Her broad impact to botany as a whole was tremendous. She was the first woman charter member of *The Botanical Society of America* and founded *The American Bryological Society.* Additionally, she was paramount in the establishment of *The New York Botanic Garden* (NYBG). Her husband

FIG. 3. Photo of Elizabeth Knight Britton peering into a microscope. Photo credit: Archives of The New York Botanical Garden. The LuEsther T. Mertz Library of The New York Botanical Garden.

Nathaniel was the first director of the NYBG (Rudolph, 1982), and Elizabeth was prominent in many aspects of this position. She was integral in the genesis and progression of the NYBG, assisting Nathaniel with the responsibilities of director in chief for 30 years. Her joint work with her husband was impressive but it did not overshadow her own work as a botanist. Elizabeth was also a conservationist (Howe, 1934), and published many papers on the need for protecting plants (including ferns) which aided in the passing of plant conservation laws in North America. Both during her career and posthumously she was recognized widely as one of the most influential and productive women in botany.

Elizabeth passed away February 25th, 1934 and a lovely memorial was written in her honor in the *Journal of The New York Botanical Garden* (Howe, 1934). Britton's philanthropic, conservation, and scientific contributions echo through the field of plant biology as a whole.

Alma Gracey Stokey (1877–1968).—When reading through literature on fern gametophytes the name Stokey is hard to miss. Alma Gracey Stokey, the mother of gametophyte morphology and anatomy, paved the way for focusing on this unique stage of the fern life cycle in the 1900s.

One of the great pteridologists of the 20th century, Stokey was born on June 17th, 1877 in Canton, Ohio to a large family of five children. Before entering college, Stokey taught at a public high school, demonstrating her passion for education and knowledge at a young age (Atkinson, 1968). Soon after her time as a teacher, she went on to receive a B.A. at Oberlin College in 1904. Stokey stayed for an additional 2 years as a research assistant in botany with Dr. Frederick Grover. She then went on to become a Ph.D. student at the University of Chicago and received her doctorate in 3 years. Although Dr. Stokey is widely known for her work on gametophytes, one of her first papers published as a Ph.D. student at the University of Chicago was on the anatomy of *Isoëtes* (Stokey, 1909). Progressing to full professor at Holyoke College in Massachusetts by 1916, she focused heavily on anatomy and morphology of fern gametophytes and used their traits to interpret the evolutionary relationships among fern lineages.

Although there is a deep literature on gametophyte morphology, her detailed approach to working with these organisms provided new perspectives and insights into this stage of the fern life cycle. Stokey made significant contributions regarding the gametophytes of many lineages of ferns including the Gleicheniaceae, Blechnaceae, Thelypteridaceae, Polypodiaceae, Dryopteridaceae, and Hymenophyllaceae (Stokey and Atkinson, 1948; Stokey, 1950, 1957; Stokey and Atkinson, 1952, 1958; Atkinson and Stokey, 1973). Her broad comparative studies including many representative species within each lineage allowed her to draw taxonomic and phylogenetic conclusions within these groups. Growing gametophytes is not a trivial task, sometimes it can take a few years for spores to germinate and mature (Stokey, 1942), thus the amount of work invested in Alma's studies was immense as documented by her numerous publications. Two of her most well cited papers include the "Comparative morphology of the

gametophyte of homosporous ferns" (Atkinson and Stokey, 1964) and "The contributions by the gametophyte to the classification of homosporous ferns" (Stokey, 1951).

Alongside Stokey was Lenette R. Atkinson, who published with her constantly. Atkinson was another prominent female pteridologist and we would be remiss to discuss gametophytes or Alma Stokey without mentioning Lenette Atkinson. Stokey and Atkinson made the botanical community aware of specific morphological, developmental, and anatomical character traits of the fern gametophyte that are taxonomically and phylogenetically informative. Some of the characters that Stokey elucidated as taxonomically important traits include thallus symmetry, hair formation, rhizoid form, and antheridial morphology. Stokey's work on gametophyte morphology, development, and anatomy has permeated the field and led to more detailed work on this life stage of ferns ranging from taxonomic treatments to physiology.

Stokey's commitment to pteridology was recognized by *The American Fern Society* in 1953, when they named her the 10th Honorary Member and the first woman to be bestowed this honor (Atkinson, 1968). Additionally, later in her career her undergraduate *alma mater* granted her an honorary doctorate degree, recognizing her foundational contributions to the field of pteridology and botany as a whole.

In addition to Dr. Stokey's focus on scientific endeavors, her outreach for women in science was demonstrated through her position at the women's college of Mount Holyoke and through her assistance with initiating the department of botany at the Women's Christian College Madras, now the Women's Christian College, Chennai, India (Atkinson, 1968). Stokey will be long-remembered for her impassioned and groundbreaking work on fern gametophytes, and her persistent dedication to the advancement of pteridology.

Norma E. Pfeiffer (1878–1978).—Norma E. Pfeiffer lived to be 100 years old and over that long time period, she contributed greatly to pteridology. A resident of the Chicago, Norma received her bachelor's and doctorate from the University of Chicago. She received her doctorate following her discovery of a new plant species *Thismia americana*, and in 1913 she was the youngest person to receive a Ph.D. from the university. Dr. Pfeiffer taught at the University of North Dakota until 1924 when she then moved to Yonkers to work at the Boyce Thompson Institute for Plant Research, which is now a part of Cornell University (The New York Times, 1989).

While she may be most well known for her discovery and breeding of lilies, Dr. Pfeiffer worked on many things pteridological such as the gametophytes of *Pteris* and *Ophioglossum* (Pfeiffer, 1912; 1916), but her foundational contribution to our field is on the genus *Isoëtes*. The first monograph of *Isoëtes* published in 1883 by Motelay and Vendryés (1883) contains beautiful illustrations and detailed species descriptions; Pfeiffer's new edition was more detailed, broader in scope, and included dichotomous keys that still prove important in morphological identification of species in the complex genus. Her monograph provided a historical perspective, introduction to the genus,

species descriptions, and many spore images (Pfieffer, 1922). Dr. Pfeiffer passed away in 1978 from complications due to a brain tumor. To date her 1922 monograph has been cited over 200 times and it remains an important reference for isoetologists.

Irene Manton (1904–1988).—An important aspect of fern biology is the rampant polyploidy that exists across nearly all major homosporous fern lineages. Among polyploid ferns, odd-numbered polyploids can have a difficult time reproducing sexually, and so adopt an apomictic life history (Grusz, 2016). Irene Manton, the mother of chromosome counts, was integral in our understanding of these two common but complex fern traits.

Irene was born on April 17th, 1904 to George and Milana Manton in the London suburb of Kensington. Her parents ensured that Irene and her older sister Sidnie received a good education, sending them to private school, taking them on many outdoor trips, and introducing them to drawing, painting, and music (Leadbeater, 2004). They also encouraged both their daughters' interest in biology; George Manton was the first to introduce Irene to a microscope, and Milana educated the girls on natural history (Preston, 1990). Irene and Sidnie were good students, they passed their college entrance exams with honors and both received scholarships (Leadbeater, 2004). Irene attended Girton College, Cambridge and it was there that her interest in chromosomes began (Preston, 1990). Some years later, after her graduate work, Irene received a postdoctoral position in Sweden and then moved to the University of Manchester for an Assistant Lectureship position in 1929. There she worked with W. H. Lang, who inspired her work on pteridophytes. In 1946, Irene took a position as the Chair of Botany at Leeds where she would remain for the remainder of her career (Leedale, 1989).

When Irene first began working with chromosomes, they were counted by staining the material of interest and then examining serial sections. Since this method was quite time consuming and not very accurate, Irene developed the "squash" method commonly used today (Preston, 1990). It was through this technique that she was able to produce the large volume of chromosome counts and cytological data needed for her influential book *Problems of Cytology and Evolution in the Pteridophyta* (Manton, 1950). This volume is also where Irene presents her scheme for apogamy in ferns, now referred to as the Döpp-Manton scheme (Cordle *et al.*, 2010; Grusz, 2016). Irene's chromosome work also helped pteridologists understand the importance of genus-level base chromosome numbers, namely through her work on *Athyrium* ($n = 40$) and *Diplazium* ($n = 41$) (Manton and Sledge, 1954).

Later in her career, Irene began to focus more on electron microscopy, with algae as her primary study organisms. While she made many important contributions to phycology (Manton and Parke, 1960; Preston, 1990), she always humbly claimed to be not a phycologist, but rather a simple botanist interested in plant cytology (Leedale, 1989).

After a brief illness in 1988, Irene passed away at the age of 84. She continued her scientific work up until a few weeks before her death (Preston, 1990). In an obituary for Irene, phycologist Gordon Leedale wrote that the

world had "...lost a scientist of genius and many of us lost a generous and steadfast friend," (Leedale, 1989).

Alice Faber Tryon (1920–2009).—Regarded as one of the 20th century's eminent pteridologists, Alice Tryon made significant contributions in the areas of fern spore morphology, taxonomy, reproductive biology, and biogeography (Fig. 4). She, alongside her husband Rolla M. Tryon Jr. (1916 – 2001), mentored and inspired a generation of pteridologists. Their lab at Harvard produced many important publications and initiated the careers of some of today's leading pteridologists (Gastony, Barrington, and Conant, 2002).

Alice Elizabeth Faber was born August 2nd, 1920 in Milwaukee, Wisconsin. She attended Milwaukee State Teachers College (now University of Wisconsin, Milwaukee) in 1941 and taught public school for several years before returning to her studies at the University of Wisconsin, Madison. It was there that she met Rolla Tryon, whom she married in 1945 (Gastony, Barrington, and Conant, 2009). As Rolla's student, Alice completed her master's degree on the spore characteristics of *Selaginella* (Tyron, 1949). Alice began her doctoral research on the genus *Pellaea* (Tryon and Britton, 1958; Tryon, 1957) at Madison, but finished her studies at Washington University in 1952 after she and Rolla moved to the Missouri Botanical Garden. A few years later, after a stint at the University of California at Berkeley, Alice and Rolla moved to Harvard University, both taking positions at the Grey Herbarium in 1958 (Gastony, Barrington, and Conant, 2009).

Through her career, Alice made numerous foundational contributions to the field of pteridology, primarily on the subjects of fern taxonomy and spores. Shortly after arriving at Harvard, Alice produced monographs of the closely related Andean genera *Jamesonia* (Tryon, 1962) and *Eriosorus* (Tryon, 1970). She hypothesized that "*Jamesonia* is derived from one or more elements in *Eriosorus*," (Tryon, 1970). Subsequent molecular analysis has provided support for Alice's hypothesis. Studies have shown the two genera to comprise one monophyletic clade; as traditionally defined, *Jamesonia* is polyphyletic and *Eriosorus* is paraphyletic (Sánchez-Baracaldo, 2004).

Alice is perhaps best remembered for her work on pteridophyte spores, a topic she returned to several times throughout her career. Her book, *Spores of the Pteridophyta* (Tryon and Lugardon, 1991) is a detailed volume on the spore features of ferns from a diversity of lineages, and includes 2,792 scanning electron microscope (SEM) images. The use of SEM for examining fern spores was pioneered by Alice during her time at Harvard (Gastony, Barrington, and Conant, 2009). She also included spore images in the book *The Ferns and Allied Plants of New England* (Tryon and Moran, 1997), an unusual but powerful tool to include in such a volume.

While Alice had many impactful solo projects, collaboration with her husband Rolla was a constant throughout her career. One of their most notable publications is *Ferns and Allied Plants with Special Reference to Tropical America* (Tryon and Tryon, 1982), a book still used today not only for identification of ferns, but to provide working taxonomic hypotheses for molecular studies (Gastony, Barrington, and Conant, 2009). The Tryons also

FIG. 4. Photo of Alice F. Tryon in the field, Brazil. Photo Credit: Mettenius - Own work, CC BY-SA 4.0, https://commons.wikimedia.org/w/index.php?curid=38789088 https://commons.wikimedia.org/wiki/File:Alicetryon_brazil.jpg

initiated many lecture series including the annual Systematics Symposium at the Missouri Botanical Garden, the New England Fern Conference, and the Tryon Lecture Series at the University of South Florida (Gastony, Barrington, and Conant, 2002). While in Florida and technically retired, the Tryons still continued to publish and engage with their community until Rolla's passing in 2001. In her last years, Alice made several generous gifts to the Field Museum in Chicago, the New England Botanical Club, the University of Vermont, and the University of Wisconsin, Madison (Gastony, Barrington, and Conant, 2009).

Alice was cared for by friends and surrounded by mementos of a happy life with Rolla when she passed away peacefully in her apartment on March 29th, 2009 (Gastony, Barrington, and Conant, 2009). Without the contributions of Alice and Rolla Tryon, pteridology would be in a very different place today. We would lack a large body of knowledge generated by their lab, as well as some of the leading fern researchers and mentors to the next generation of pteridologists.

Barbara Joe Hoshizaki (1928–2012).—Barbara Joe Hoshizaki was a world expert in fern horticulture. Her book, the *Fern Growers' Manual*, is the preeminent volume on the subject. The second edition of the book, co-authored with Dr. Robbin C. Moran, contains information on about 700 species of ferns from 124 genera (Hoshizaki and Moran, 2001). Throughout her life, Barbara contributed greatly to not only our knowledge of fern horticulture, but taxonomy and popular interest in ferns as well. She published numerous papers on the cultivation of ferns (Hoshizaki, 1970b; 1981; Hoshizaki and Wilson, 1999; Yansura and Hoshizaki 2012), fern hybrids (Hoshizaki, 1991; 1975), and systematics and identification of ferns — notably of *Platycerium* (Hoshizaki, 1970a; 1972; Hoshizaki and Price, 1990).

Barbara's interest in pteridophytes began when she attended the University of California, Los Angeles in 1951. There she received her bachelor's degree and met Mildred Mathias, who would become Barbara's mentor and prime advocate for her study of ferns (Moran, 2012). Mildred herself was an incredibly influential botanist in her own right: an Apiaceae expert and important founding member of the Organization for Tropical Studies (Gibson, 2017).

In 1954, Barbara received her master's degree from the University of California, Los Angeles (UCLA) and became a professor of biology at the City College of Los Angeles, where she would remain for 28 years. In addition to teaching, Barbara was the Curator of Ferns at the UCLA Herbarium; she served as the president of the American Fern Society, Southern California Horticultural Institute, and Los Angeles International Fern Society; and was the vice-president for the Pacific Horticultural Foundation (Moran, 2012).

In 1967, Barbara spent six weeks on the first Organization for Tropical Studies Ferns and Lycophytes course (Moran, 2012). This experience was so meaningful to her that after her passing in 2012, her family established the Barbara Joe Hoshizaki Memorial Scholarship to aid students in attending OTS courses. [As an aside, the authors of this paper were fortunate enough to

receive this scholarship for the 50th anniversary of the Tropical Ferns and Lycophytes course in 2017, an opportunity for which we are extremely grateful.] Through her numerous publications and support of organizations like OTS, Barbara's memory and contributions to the fern community live on.

Florence Wagner (1919–).—Florence Wagner (née Signaigo) was born in 1919. In the 1940s she attended graduate school at the University of California, Berkeley. It was there that she met Warren "Herb" Wagner. They married in 1948, beginning a long and fruitful career of collaboration (Farrar, 2002). Florence was trained as a phycologist, and remarked that she would happily study ferns as long as Herb kept her away from the coasts (Christopher Haufler, personal communication). Florence and Herb helped increase pteridologist's interest in hybrids, publishing review and novel empirical papers on the subject (Wagner and Wagner, 1979; Wagner *et al.*, 1992)

In the obituary written for Herb Wagner in the American Fern Journal, Don Farrar shares a touching anecdote about the Wagners:

> "The excitement of field trips with Herb and Florence remain highlights of my graduate years at Michigan, as do warm memories of holidays at the Wagner home, cutting out snowflakes or whatever project Florence had designed for their 'extended family' of graduate students. This nurturing of an Ozark farm boy a long way from home made a difference. It was a personal gift. Yet I know it was only one of many such personal gifts, bestowed on many others as well, by Herb and Florence. For those gifts we all say thanks!" — (Farrar, 2002)

Florence is still alive today at 100 years old (summer 2019).

Conclusion

The women highlighted here contributed broadly to our field and have inspired many generations of past and current pteridologists. Their work spans the spectrum of biology from anatomy to systematics and cytology to horticulture. Through our review of their work we have tried to exemplify not only their impact on our field, but also their lives and achievements as people and scientists.

In addition to the female pteridologists we have covered in detail, there are many women whose contributions were impactful, but were not detailed in this short review. A handful of these women include: Doris Löve, who published the greatly influential volume, *A Cytotaxonomic Atlas of the Pteridophyta* (Löve, Löve, and Pichi-Sermolli, 1977; Kaersvang, Weber, and Ives, 2000) with her husband Áskell, as well as having a second career as a translator for 12 languages (Löve, Löve, and Pichi-Sermolli, 1977; Kaersvang, Weber, and Ives, 2000); Diana Stein, one of the first people to work on fern chloroplasts, investigating their structure, component genes, and evolutionary signal (Palmer and Stein, 1982; Stein, Palmer, and Thompson, 1986; Stein and Barrington, 1990); Gillian Cooper-Driver, who conducted work on secondary compounds in bracken (*Pteridium*) and their variation in the context of

phenology, herbivory, and taxonomy (Cooper-Driver 1976; Cooper-Driver and Swain 1976; Cooper-Driver *et al.* 1977); Aura Star, who researched frond exudates and allelopathy in *Pityrogramma* (Star and Mabry, 1971; Star, 1980); and Margaret Slosson, whose book *How Ferns Grow* (Slosson, 1906) was one of the first on pteridophyte development, and her work on fern hybridization was the first empirical evidence of such contributed by an American researcher (Slosson, 1902; Clute, 1902).

The history of early women in pteridology is quite distinctive in STEM and this is reflected in the current state of our field. Today there are numerous labs run by prominent female pteridologists all over the world, all contributing regularly to our growing knowledge of ferns. With this paper we bring to light the foundational women, the work they contributed to fern biology, and the fruitful collaborations they had with their peers; we hope that they continue to inspire young scientists to enter our unique field of pteridology.

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Jamesonia ×*intermedia*: A New Hybrid Between *J. biardii* and *J. insignis* (Pteridaceae) from Brazil

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Abstract.—This paper describes and illustrates a new hybrid, *Jamesonia* ×*intermedia*, from Serra dos Órgãos, Rio de Janeiro State, Brazil. The hybrid, most of whose spores are aborted, shows intermediate morphology between its putative parents (*J. biardii* and *J. insignis*) in lamina dissection, shape of the ultimate segments, and pubescence of the adaxial surface of the pinnae and rachises.

Key Words.—Brazilian Atlantic Rainforest, *Eriosorus*, ferns, hybridization, Pteridoideae

Jamesonia Hook. & Grev., a member of subfamily Pteridoideae in the Pteridaceae, comprises about 50 species, with a geographical distribution restricted to the Neotropics (Schuettpelz *et al.*, 2007; Zhang *et al.*, 2017; PPG I, 2016). Most of the species of this genus occur in the Andean páramos and subpáramos, from 800 to 5000 m in elevation. In Brazil, seven species and one hybrid are known; they occur mainly in the Brazilian Atlantic Rainforest, in Campos de Altitude and cloud forests, above 1500 m in elevation (Della and Prado, in preparation).

In the last decades, the delimitation of *Jamesonia* has changed considerably, with the inclusion of *Eriosorus* Fée (Sánchez-Baracaldo, 2004a; 2004b) and the segregation of *Tryonia* Schuettp., J. Prado & A. T. Cochran (Cochran *et al.*, 2014). Thus, in the present circumscription (sensu PPG I, 2016), the genus can be recognized by having 1–6-pinnate, triangular, linear, or less often narrowly triangular, and narrowly elliptic, erect to scandent laminae, and by the brown rachises.

Hybridization is common in *Jamesonia*. Tryon (1962; 1970), in her monographs of the genera *Jamesonia* and *Eriosorus*, described nine hybrids (*Eriosorus hirtus* var. *gladulosus* × *E. flexuosus* var. *flexuosus*, *E. hispidulus* var. *hispidulus* × *Jamesonia* sp., *E. warscewiczii* × *J. scammanae*, *E. cheilanthoides* × *J. brasiliensis*, *E. cheilanthoides* × *Jamesonia* sp., *E. cheilanthoides* × *E. flexuosus* var. *flexuosus*, *E. flexuosus* var. *flexuosus* × *E. warscewiczii*, *E. flexuosus* var. *flexuosus* × *E. paucifolius*, and *E. glaberrimus* × *E. congestus*), besides five morphological "variants" (involving the species *E.*

hispidulus, *E. novogranatensis*, *E, rufescens*, *E. hirsutulus*, and *E. flexuosus*). Among these hybrids, only one was reported from Brazil: *E. cheilanthoides* × *J. brasiliensis*. These "variants" (the term used by Tryon) can be considered hybrids because they have aborted or irregular spores. Tryon (1962; 1970) verified the presence of abortive spores or/and the failure of chromosome pairing in the meiotic cells of all hybrids described.

During the preparation of the taxonomic treatment of *Jamesonia* for the Flora of Brazil 2020 (online), a large population of a new hybrid was found. The main goal of the present paper is to describe this new hybrid, based on the material collected recently in the Serra dos Órgãos, Rio de Janeiro State, Brazil.

Materials and Methods

Specimens were collected at the Pico do Alcobaça, Serra dos Órgãos, Petrópolis (Rio de Janeiro, Brazil) and were deposited at NY, RB, SP, and SPF (herbarium acronyms according to Thiers (2019), continuously updated).

Morphological terms follow Lellinger (2002) and Tryon and Lugardon (1990). Scanning electronic microscopy (SEM) analyses were carried out to verify spore morphology. The spores were not submitted to any chemical treatment. Samples from three specimens were fixed on stubs using double-sided tape and then each stub was metalized with gold and analyzed under the SEM (Philips XL30).

The distribution map was drawn using the software ArcGIS v. 10.5 (ESRI, 2016). The shape files of Brazil and Conservation Units were obtained form IBGE (2015) and ICMBio (2019) websites, respectively.

Results and Discussion

Jamesonia* ×*intermedia A.P. Della & J. Prado, **hyb. nov.** Type.—BRAZIL. Rio de Janeiro: Petrópolis, Parque Nacional da Serra dos Órgãos, Bom Fim, Pico do Alcobaça, 22°28′22.9″S, 43°07′00.4″W, 1689 m, 27 Feb 2019, *A.P. Della et al. 69* (holotype: SP; isotypes: NY, RB, SPF). (Figs. 1G–L, 2–5).

Diagnosis.—*Jamesonia* ×*intermedia* can be recognized in having 2-pinnate-pinnatisect to 3-pinnate-pinnatifid laminae; triangular and coriaceous pinnae, with adaxial surface glabrous or with sparse hairs, abaxial surface moderately covered by hairs; flexuous rachises, costae, and costules, stramineous in young plants and brown in adult plants; and elongate-triangular to ovate ultimate segments, with crenate margins. In addition, the spores of the hybrid are "withered" and empty.

Plants terrestrial or rupicolous. **Rhizomes** short-creeping, 2.5–3.0 mm diam., densely covered by hairs and bristles, the hairs dark brown, multicellular, glandular, 0.2–2.2 mm long, the bristles dark brown, with darker-colored thickened transverse cell walls, apex long-filiform, base with 2–5 cells wide, apical cell globose, 1.3–2.4 mm long. **Fronds** monomorphic, 83.0–125.0 ×

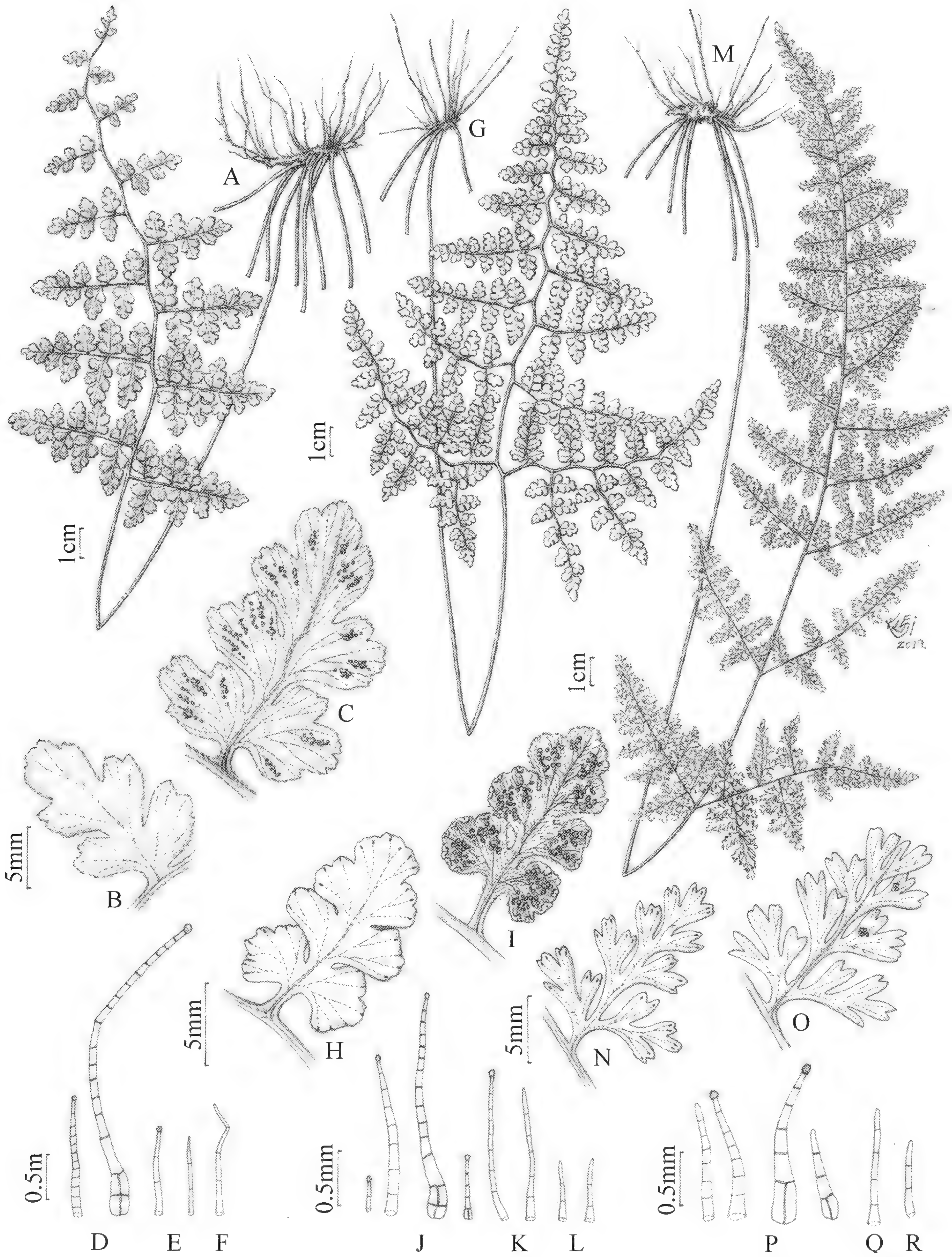

FIG. 1. **A–F**. *Jamesonia insignis*. **A**. Habit. **B, C**. Adaxial and abaxial surfaces of the pinnule, respectively. **D**. Hairs and bristles of the rhizome. **E**. Hairs of the petiole. **F**. Hair of the rachis and lamina. **G–L**. *J.* ×*intermedia*. **G**. Habit. **H, I**. Adaxial and abaxial surfaces of the pinnule, respectively. **J**. Hairs and bristles of the rhizome. **K**. Hairs of the petiole. **L**. Hairs of the lamina. **M–R**. *J. biardii*. **M**. Habit. **N, O**. Adaxial and abaxial surfaces of the pinnule, respectively. **P**. Hairs and bristles of the rhizome. **Q**. Hairs of the petiole and rachis. **R**. Hairs of the lamina. **A–F**. *J. Prado et al. s.n.* (SPF 60080). **G-L**. *A.P. Della et al. 69* (SP). **M–R**. *A.C. Brade 16515* (RB).

FIG. 2. **A–G**. *Jamesonia* ×*intermedia*. **A–C**. Habit. **D, E**. Adaxial and abaxial surfaces of the pinna, respectively. **F**. Fertile pinnae. **G**. Young frond. **A, F**. J.M. Braga. **B–E, G**. A.P. Della.

13.0–19.5 cm; **petioles** semi-cylindrical, adaxially grooved, 60.0–92.5 cm × 0.6–1.6 mm, bicolorous on young plants and uniformly brown on older plants, glabrous to moderately covered by hairs on both surfaces, the hairs with 0.3–1.6 mm long, glandular or eglandular, hyaline to castaneous, sometimes bicolorous, erect, multicellular; **laminae** 2-pinnate-pinnatisect to 3-pinnate-pinnatifid, triangular, semi-scandent, gradually tapering towards the apex

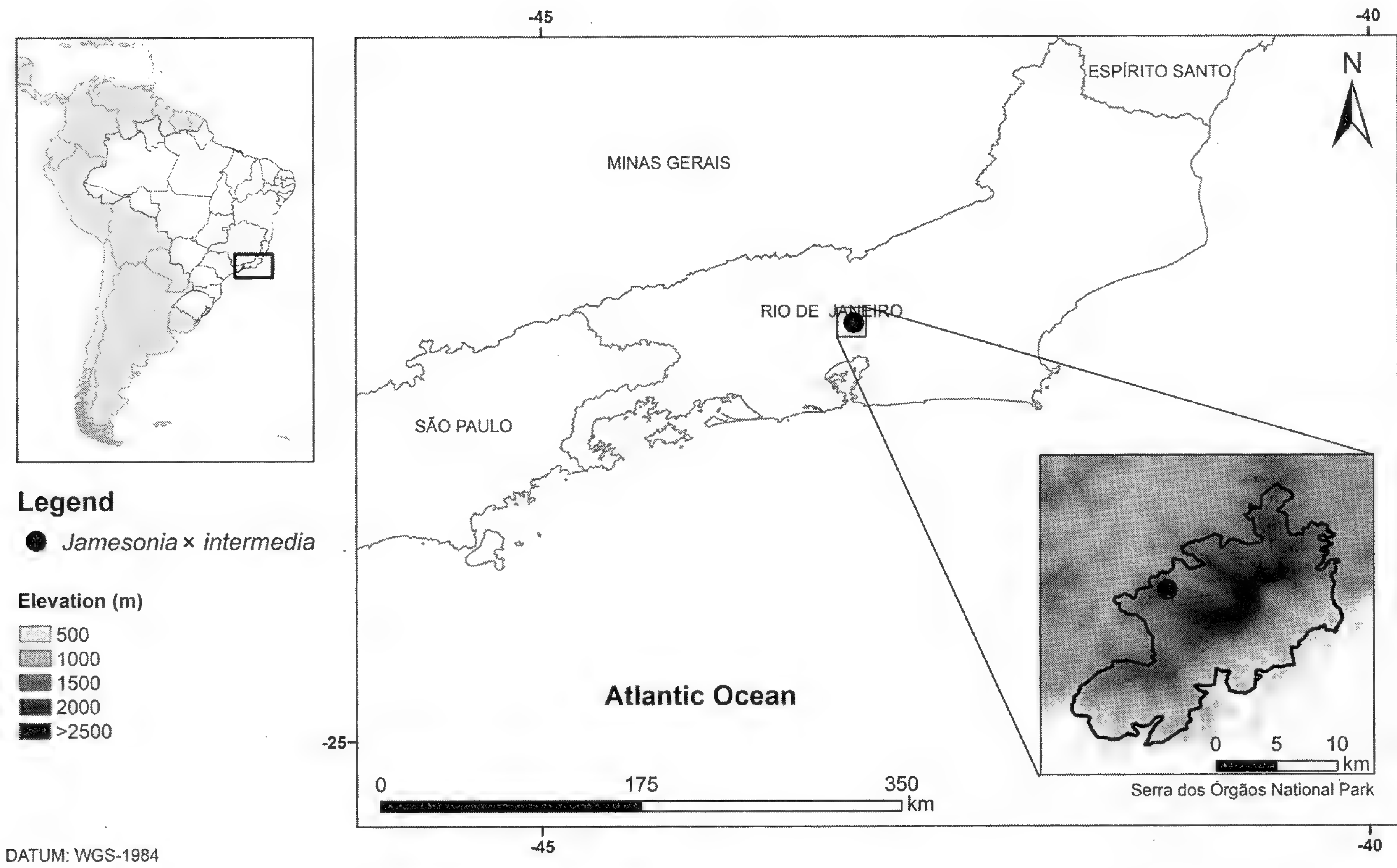

FIG. 3. Distribution of *Jamesonia* ×*intermedia* in Brazil.

(long-attenuate, pinnatisect), with usually 10–12 pairs of lateral pinnae, 18.0–32.5 × 13.0–19.5 cm, coriaceous; **rachises**, **costae** and **costules** flexuous, semi-cylindrical, adaxially grooved, green to stramineous on young plants and uniformly brown on older plants, abaxially and adaxially glabrous to sparsely covered by hairs, mainly in the groove and on the axils of the pinnae, the hairs eglandular, similar to those of the petioles; **pinnae** usually ascending, triangular, the basiscopic side slightly larger, 5.0–12.5 × 3.5–8.0 cm, alternate, long-stalked, the stalk 9.0–27.0 mm long, 0.6–1.2 mm diam, semi-cylindrical, adaxially grooved, stramineous to brown, adaxial surface of the pinnae glabrous or less often sparsely covered by hairs, abaxial surface sparsely to moderately covered by hairs, mainly on the veins, the hairs eglandular, similar to those of the petioles; **primary pinnules** triangular, sometimes ovate, 1.2–4.5

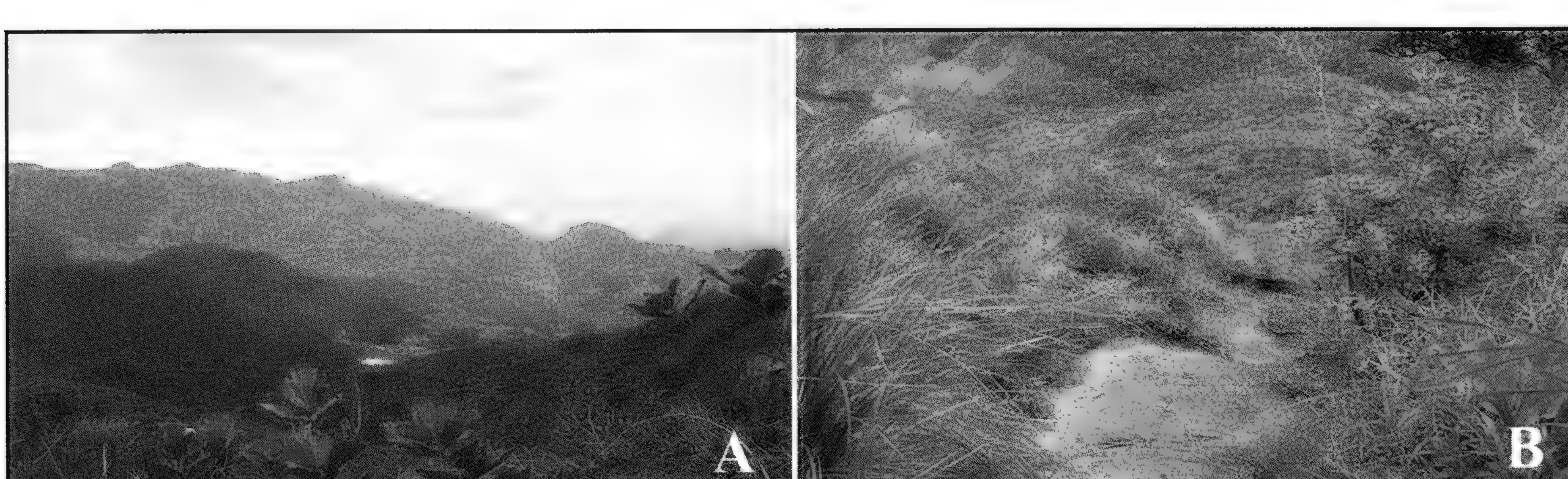

FIG. 4. **A**, **B**. Habitats of *Jamesonia* ×*intermedia*. **A**. View of the Pico do Alcobaça, Serra dos Órgãos, Rio de Janeiro State. **B**. Trail to the Pico do Alcobaça. **A, B**: A.P. Della.

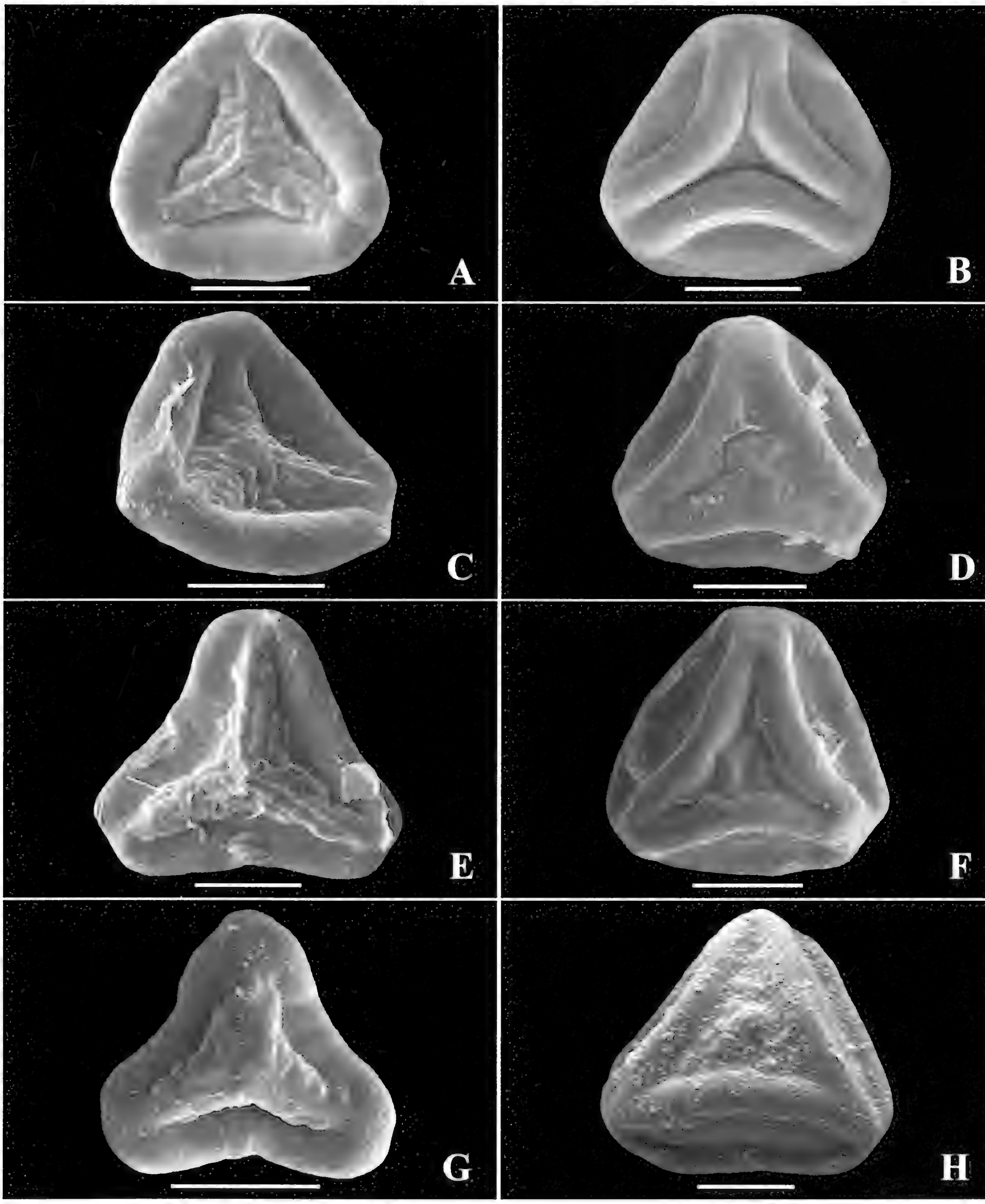

FIG. 5. SEM photomicrographs of *Jamesonia ×intermedia* spores. **A–D**. Irregular spores. **E–H**. Regular spores. Left column showing proximal surface, right column showing distal surface. Scale bars = 20 μm. **A**, **C–G**. *A.P. Della et al. 69* (SP). **B**. *A.P. Della et al. 72* (SP). **H**. *A.P. Della et al. 67* (SP).

× 1.0–3.7 cm, alternate, stalked, the stalk 4.0–1.2 mm long, 0.6–0.8 mm diam, semi-cylindrical, adaxially grooved, green, stramineous to brown; **secondary pinnules or segments** triangular to ovate, 0.4–1.5 × 0.4–1.0 cm; margins crenate, often recurved; **veins** usually furcate, with enlarged clavate tips

reaching the laminae margin. **Sori** on the veins, forming several lines along the segments; **spores** mostly abortive, dark brown, proximal surface with coalescent ridges, mainly near trilete aperture, distal surface laevigate, 40.0–60.0 μm. diam.

DISTRIBUTION AND HABITAT.—*Jamesonia* ×*intermedia* is semi-scandent and grows on the edge of trails, in a partially shaded location, between grasses and bromeliads, in the Pico do Alcobaça, Serra dos Órgãos, Rio de Janeiro State (Fig. 2), at 1650–1689 m elevation (Figs. 3 and 4). The soil of this region has a broad rocky base, and a thin layer of dark organic matter, often moist.

ETYMOLOGY.—The specific epithet refers to the presence of intermediate morphological characters between the putative parentals.

PARATYPES.—Brazil. Rio de Janeiro: Petrópolis, Parque Nacional da Serra dos Órgãos, Bom Fim, Pico do Alcobaça, 22°28′22.9″S, 43°07′00.4″W, 1689 m, 27 Feb 2019, *A.P. Della et al. 67* (SP); idem, *A.P. Della et al. 68* (SP); idem, *A.P. Della et al. 70* (SP); idem, *A.P. Della et al. 72* (SP); idem, 22°28′17″S, 43°07′00″W, 1650 m, 04 Jun 2017, *J.M.A. Braga 17-002* (RB).

This hybrid shows morphology intermediate between *Jamesonia insignis* (Mett.) Christenh. and *J. biardii* (Fée) Christenh. (See Table 1 and Fig. 1). It more closely resembles *J. insignis* than *J. biardii* in the size and shape of the pinnae, pinnules, and ultimate segments, as well as crenate margins of the laminae. On the other hand, it resembles *J. biardii* by the glabrous or rarely sparsely eglandular hairs on the adaxial surface of the laminae and glabrous to sparsely eglandular hairs on the rachises.

Jamesonia ×*intermedia* is currently known only in the Serra dos Órgãos, Rio de Janeiro State. However, its occurrence in other places where its putative parents occur, is probable.

In scanning electron microscope analyses, most of the spores are "withered" (Fig. 5). The spores appear to have a cavity (concave aspect) on the proximal surface (Fig. 5A, C), probably due to the absence of content. These irregular spores measure 40.0–50.4 μm. Some spores showed "regular" (turgid) morphology (Fig. 5E-H) and measure 49.9–60.0 μm. The size of these "regular" spores is similar to those of *J. insignis* and *J. biardii.*

The region of Petrópolis, and specifically around the Pico do Alcobaça, has been impacted by agriculture. As the hybrid was found only in a single population in the Pico, further human impacts could put the population at risk. Another possible threat is fire, which this year burned several areas around to the Parque Nacional da Serra dos Órgãos.

Individuals of the putative parental species were not found close to the hybrid population. The populations of the putative parents, *Jamesonia insignis* and *J. biardii,* occur only in more preserved environments in the same locality, whereas the hybrid occurs in one disturbed area. Other species of *Jamesonia* do occupy the locality of the hybrid population: *J. brasiliensis* Christ, *J. cheilanthoides* (Sw.) Christenh. and *J. rufescens* (Fée) Christenh., but they have morphology quite distinct of the putative parents and the hybrid

TABLE 1. Morphological comparison among *Jamesonia insignis*, *J. biardii* and the new hybrid.

Characters	Taxa		
	J. insignis	*J. ×intermedia*	*J. biardii*
Rhizome indument	Glandular hairs and bristles	Glandular hairs and bristles	Glandular and eglandular hairs and bristles
Habit/frond size	Semi-scandent 35.0–105.0 × 6.0–20.5 cm	Semi-scandent 83.0–125.0 × 13.0–19.5 cm	Erect to slightly arcuate 20.0–78.0 × 5.6–11.5 cm
Petiole size and indument	16.0–63.0 × 1.0–2.0 cm Sparsely to moderately covered by glandular and eglandular hairs	6.0–92.5 × 0.6–1.6 cm Glabrous to moderately covered by glandular and eglandular hairs	10.0–30.0 × 1.0 cm Glabrous to sparsely covered by eglandular hairs
Lamina dissection and shape	2-pinnate-pinnatisect to 3-pinnate-pinnatisect Triangular	2-pinnate-pinnatisect to 3-pinnate-pinnatifid Triangular	2-pinnate-pinnatisect Elongate-triangular
Lamina texture	Chartaceous	Coriaceous	Chartaceous
Rachis shape and indument	Flexuous Moderately covered by eglandular hairs	Flexuous Glabrous to sparsely covered by eglandular hairs	Straight Glabrous to sparsely covered by eglandular hairs
Pinna size, shape and indument	2.1–17.5 × 1.2–8.3 cm Triangular Adaxial moderately covered by eglandular hairs Abaxial moderate to densely covered by eglandular hairs	5.0–12.5 × 3.5–8.0cm Triangular Adaxial glabrous to sparsely covered by eglandular hairs Abaxial sparse to moderately covered by eglandular hairs	1.0–3.0 × 0.5–2.3 cm Triangular Adaxial and abaxial glabrous to sparsely covered by eglandular hairs
Stalk of pinna size	2.3–11.0 × 0.1–0.7 mm	9.0–27.0 × 0.6–1.2 mm	1.0–3.0 × 0.6 mm
Ultimate segments shape	Ovate to orbiculate	Elongate-triangular to ovate	Bifurcate
Lamina margin	Crenate to denticulate-crenate	Crenate	Entire
Spore size and morphology	67.1–67.8 µm Proximal surface with coalescent ridges, distal surface rugose	Irregular: 40.0–50.4 µm Regular: 49.9–60.0 µm Proximal surface with coalescent ridges, distal surface laevigate	53.7–57.5 µm Proximal surface tuberculate, distal surface rugose

specimens. Thus, we do not think they are involved with formation of the hybrids.

According to our observations of the population of this hybrid in the field, the plants multiply vegetatively by the growth of the rhizomes.

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Silica Bodies in *Selaginella* (Selaginellaceae)

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Abstract.—The microphylls of *Selaginella* bear structures that have been given names as diverse as idioblasts, papillae, sclereids, fibers, and warts, yet they resemble silica bodies. However, for most species of the genus, no study has ever shown the composition of these structures or proven their nature comprehensively. Based on scanning electron microscopy and energy dispersive X-ray spectroscopy analyses, we confirmed the presence of silica bodies in microphylls of *Selaginella*, described four distribution patterns of the structures, and carried out a terminology review. The presence of silica may be related to mechanical protection of the cell wall, activation of defense mechanisms, and providing support for microphylls. Further in-depth analyses based on studies on the evolution of this character remain necessary to elucidate its relevance for the ecological relationships and systematics of *Selaginella*.

Key Words.—Lycophytes, silicon, microphylls, taxonomy.

Silicon is the major inorganic constituent of vascular plants, occurring in the plant body in the form of silica gel or silica bodies (Chauhan *et al.,* 2011; Frantz *et al.,* 2011; Gibson, 1893; Kim *et al.,* 2002; Piperno and Pearsall, 1998; Sundue, 2009), having the dual functions of resistance and protection, especially against herbivores, pathogens, and unfavorable climatic conditions such as drought (Chauhan *et al.,* 2011; Ma and Yamaji, 2008; Moraes *et al.,* 2004). During water uptake by roots, silicon is absorbed in the form of monosilicic acid and deposited in various cell types, such as parallelepipedal bulliform cells, silica short cells, long sinuous-walled epidermal cells, and prickle hairs, all of which are called phytolites (Chauhan *et al.,* 2011).

Silica bodies may aid taxonomic studies on ferns and lycophytes (Iriarte and Paz, 2009; Kaufman *et al.* 1971; Ma and Takahashi, 2002; Mazumdar, 2011; Ribeiro, Santos, and Moraes, 2007; Sundue, 2009). These structures have been frequently reported, for instance, associated with vegetative organs of *Selaginella* P. Beauv. (Gibson, 1893; Gibson, 1894; Mazumdar, 2011; Ogura, 1972; Piperno, 1988). However, only Dengler and Lin (1980) and Trembath-Reichert *et al.* (2015) have actually performed specific tests for the presence of silica; yet, both those studies lack significant sampling. Thus, no systematic survey has been performed on either the presence or distribution of silica bodies in most species of the genus. These aspects limit the use of this

character for taxonomic purposes in *Selaginella* in view of the high species richness of the genus (ca. 700 species [PPG I, 2016] currently distributed among seven subgenera of wide distribution [Weststrand and Korall, 2016b]). Herein, we establish a distribution pattern based on the infrageneric classification proposed by Weststrand and Korall (2016b).

Another aspect that hampers the use of silica bodies in *Selaginella* is the adoption of varied terminologies by different authors. Some studies have reported the presence of structures on the surface of microphylls assuming that they could have siliceous composition, calling them "warty sclereids" (Dengler, 1980), "warty fibers" (Dahlen, 1988), "epidermal warts" (Bienfait and Waterkeyn, 1974), "papillate cells" (Góes-Neto, Assis, and Salino, 2017), "papillate idioblast-like cells" (Valdespino, López, and Góes-Neto, 2014) or "elongate, papillate cells" (Valdespino, 2015a,b). Valdespino (2015c) has synonymized papillate cells and idioblasts, "elongate, idioblast-like papillate cells" (Valdespino *et al.,* 2015), "idioblasts" (Cremers and Boudrie, 2007; Góes-Neto and Salino, 2018; Góes-Neto, Heringer, and Salino, 2015; Valdespino, 2017a), "papillae" (Valdespino, 2017a,b) and "papillate idioblasts" (Valdespino, López, and Ceballos, 2018). We analyzed the images shown in the above mentioned studies to confirm whether the authors were actually referring to a same type of structure, therefore, it is noted that no formal systematized terminology was used by the authors. The use of all such diverse terms renders it impossible to standardize the use of silica bodies for taxonomic purposes.

Despite the fact that silica bodies can be easily observed on the leaf epidermis, conceptual discrepancies are frequently found in the literature due to the lack not only of anatomical, chemical, and radiological analyses on these structures but also of a clear description of their possible distribution patterns in *Selaginella*. Aiming to fill both these gaps on the knowledge of silica bodies in the genus, we conducted a comparative analysis of microphylls by sampling five of the *Selaginella* subgenera proposed by Weststrand and Korall (2016b), seeking to investigate the presence and distribution of silica bodies in the genus as well as to reinterpret these characters.

Material and Methods

Taxa sampling.—The sampling for analysis of microphyll epidermal cells encompassed 55 species from five out of the seven *Selaginella* subgenera: two species from *S.* subg. *Exaltatae*, 13 from *S.* subg. *Gymnogynum,* three from *S.* subg. *Rupestrae,* one from *S.* subg. *Selaginella* and 38 from *S.* subg. *Stachygynandrum*, following Weststrand and Korall (2016a, b). The studied species with their respective taxon authorships, collectors, and herbaria where specimens are deposited are summarized in Table 1. Herbarium acronyms follow those of Thiers (2019, continuously updated).

Scanning electron microscopy.—To remove organic matter, dorsal and lateral microphylls were subjected to incineration with a 3:1 solution of perchloric acid and nitric acid for six hours. Subsequently, they were heated on a hot plate at 80° C for three hours, after which hydrogen peroxide was

added to the solution. After two hours, samples were washed in distilled water (five times, 5 minutes each) through centrifugation. For SEM observation, samples in distilled water were pipetted directly onto stubs. Dorsal and lateral microphyll samples were obtained from herbarium specimens and placed onto stubs, which had been previously coated with double-sided carbon tape. In both methods, stubs were sputter-coated with gold in an Emitech K550 sputter coater and were then examined and photographed at different magnifications in a TESCAN MIRA3 scanning electron microscope at 15 kV acceleration voltage.

Energy-dispersive X-ray spectroscopy.—EDS chemical microanalyses were performed in solid cellular inclusions with a PentaFET Precision X-ray detector coupled with the same microscope and under the same operating conditions for capture of electron micrographs, allowing for qualitative analysis of the chemical composition as well as semiquantitative atomic composition analysis of samples. Absorbance peaks indicating relative elemental chemical concentration $\geq$ 0.5% and error interval of 0-1 were considered significant.

Phytolith description and nomenclature.—Morphological classification of silica bodies followed the International Code for Phytolith Nomenclature 1.0 (ICPN) (Madella, Alexandre, and Ball, 2005).

Results

Chemical microanalyses (EDS) confirmed the siliceous composition (Fig. 1A-1F) of structures in the following representatives of the analyzed subgenera: *S. simplex* Baker and *S. willdenowii* (Desv. ex Poir.) Baker (subg. *Stachygynandrum*), *S. conduplicata* Spring (subg. *Gymnogynum*), *S. anaclasta* Alston ex Crabbe & Jermy (subg. *Exaltatae*), and *S. rupestris* (L.) Spring (subg. *Rupestrae*), except in *S. selaginoides* (L.) P. Beauv. ex Schrank & Mart. (subg. *Selaginella*). Silica bodies were observed on the epidermis of all species, with distinct distribution patterns, and always in the form of conical projections (Fig. 2A-2B), except in *S. beitelii* A. R. Smith and *S. willdenowii* (subg. *Stachygynandrum*), *S. selaginoides* (subg. *Selaginella*) and *S. silvestris* Aspl. (subg. *Gymnogynum*), in none of which silica bodies were seen on the leaf surface. We found no exclusive pattern to any subgenus, but we did observe four distribution patterns of silica bodies in relation to the microphyll region (margin, intermediary portion and midrib) according to the species: medial-marginal, laminar, marginal and medial-costal. These patterns are described below and their occurrence among the studied species is summarized in Table 2.

Medial-marginal (Fig. 3A–3B).—Silica bodies restricted to the margin and intermediary region of the microphyll.

Laminar (Fig. 3C–3D).—Silica bodies distributed across all regions of the microphyll.

Marginal (Fig. 3E–3F).—Silica bodies restricted to the microphyll margin.

TABLE 1. Taxa analyzed and voucher specimen selected for the research.

Taxa	Voucher specimen
***Selaginella* subg. *Exaltatae* Weststrand & Korall**	
S. anaclasta Alston ex Crabbe & Jermy	P. Labiak *et al.* 5639 (RB)
S. exaltata (Kunze) Spring	G. T. Prance *et al.* s.n. (MG)
***Selaginella* subg. *Gymnogynum* (P.Beauv.) Weststrand & Korall**	
S. asperula Spring	O. C. Nascimento 541 (MG)
S. conduplicata Spring	S. Maciel 1628 (MG)
S. epirrhizos Spring	F. Bisby *et al.* (MG)
S. fragilis A. Braun	A. S. L. da Silva *et al.* 408 (MG)
S. geniculata (C. Presl) Spring	A. H. G. Alston 7778 (MG)
S. kraussiana (Kunze) A. Braun	N. Rosa & J. M. Pires 3885 (MG)
S. lingulata Spring	A. G. H. Alston 8344 (MG)
S. marginata (Humb. & Bonpl. ex Willd.) Spring	O. S. Ribas *et al.* 5137 (MG)
S. parviarticulata W.R. Buck	R. Viveros 251 (BHCB)
S. parkeri (Hook. & Grev.) Spring	M. R. Pietrobom 7160 (MG)
S. suavis (Spring) Spring	E. P. Heringer 1522 (MG)
S. sulcata (Desv. ex Poir.) Spring ex. Mart.	J. J. Strudwick *et al.* 3694 (MG)
S. silvestris Aspl.	A. H. G. Alston 7128 (MG)
S. tomentosa Spring	A. H. G. Alston 8634 (MG)
***Selaginella* subg. *Rupestrae* Weststrand & Korall**	
S. sartorii Hieron.	A. H. G. Alston 6513 (MG)
S. sellowii Hieron.	A. H. G. Alston 6382 (MG)
S. rupestris (L.) Spring	F. G. Schroeder 6022 (MG)
***Selaginella* subg. *Selaginella* P.Beauv.**	
S. selaginoides (L.) P. Beauv. ex Schrank & Mart.	W. Repetzky s.n. (MG)
***Selaginella* subg. *Stachygynandrum* (P.Beauv. ex Mirb.) Baker**	
S. amazonica Spring	G. T. Prance *et al.* s.n. (MG)
S. apoda (L.) C. Morren	S. W. Leonard 4868 (MG)
S. applanata A. Braun	H. P. Bautista 82 (MG)
S. beitelii A.R. Sm.	F. A. Carvalho *et al.* 353 (INPA)
S. bombycina Spring	A. H. G. Alston 7859 (MG)
S. brevifolia Baker	J. M. Poole 1948 (MG)
S. breynii Spring	C. A. Cid 531 (MG)
S. coarctata Spring	G. T. Prance *et al.* (MG)
S. contigua Baker	C. A.W. Schvacke 952 (MG)
S. convoluta (Arn.) Spring	G. J. Shepherd *et al.* (MG)
S. decomposita Spring	A. C. Brade 20208 (MG)
S. erythropus (Mart.) Spring	M. R. Pietrobom 5553 (MG)
S. falcata (P. Beauv.) Spring	H. S. Irwin *et al.* (MG)
S. flagellata Spring	T. Plowman *et al.* (MG)
S. flexuosa Spring	A. C. Brade 16585 (MG)
S. homaliae A. Braun	D. W. Stevenson *et al.* 978 p. p. (INPA)
S. kochii Hieron.	L. A. Maia *et al.* 327 (MG)
S. lechleri Hieron.	M. R. Pietrobom 7003 (MG)
S. microdonta A.C. Sm.	P. Cavalcante 3056 (MG)
S. microphylla (Kunth) Spring	A. H. G. Alston 6703 (MG)
S. minima Spring	J. Pallos & M. R. Pietrobom 103 (MG)
S. mucugensis Valdespino	F. S. Gomes *et al.* 574 (ALCB)
S. muscosa Spring	M. R. Pietrobom & L. F. G. Gomes 4628 (MG)

TABLE 1. Continued.

Taxa	Voucher specimen
S. nanuzae Valdespino	A. Salino *et al.* 7788 (BHCB)
S. pallescens (C. Presl) Spring	A. H. G. Alston 5535 (MG)
S. potaroensis Jenman	A. H. G. Alston 5318 (MG)
S. producta Baker	M. R. Pietrobom 7044 (MG)
S. pulcherrima Liebm.	R. C. Moran 5523 (MG)
S. radiata Baker	A. J. Arruda *et al.* 949 (MG)
S. revoluta Baker	B. Maguire *et al.* (MG)
S. rhodostachya Baker	E. Ule 8491 (MG)
S. seemannii Baker	A. H. G. Alston 8632 (MG)
S. simplex Baker	A. L. Ilkiu-Borges *et al.* s/n (MG)
S. tenuissima Fée	W. A. Egler 483 (MG)
S. willdenowii (Desv. ex Poir.) Baker	S. Maciel 1644 (MG)

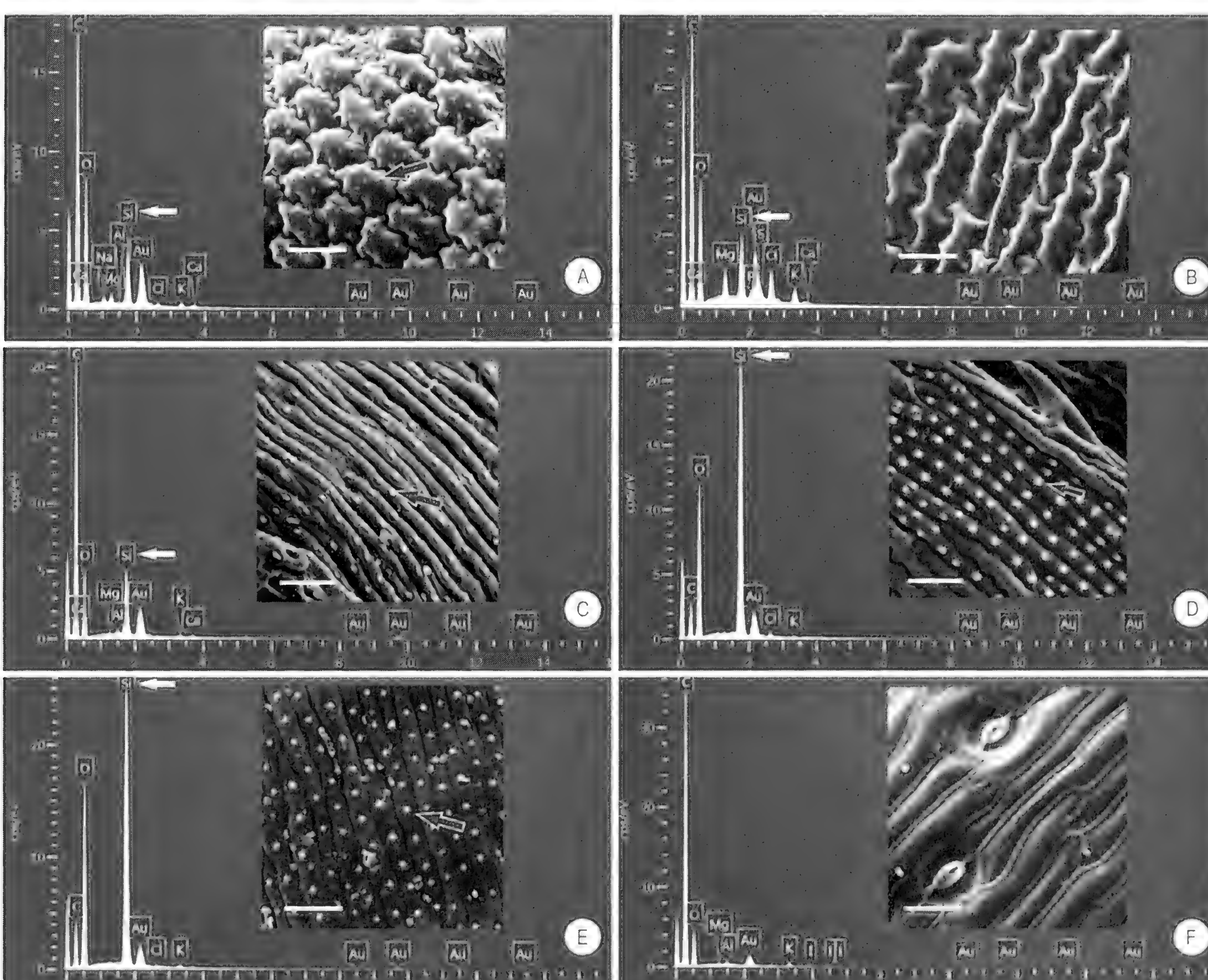

FIG. 1. Energy dispersion X-ray spectroscopy of epidermal cells on *Selaginella* microphylls, confirming that the structures are silica bodies. **A**. *Selaginella simplex*. **B**. *S. wildenowii*. **C**. *S. anaclasta*. **D**. *S. conduplicata*. **E**. *S. rupestris*. **F**. *S. selaginoides*. Silica bodies (arrows). Bars: 25 μm (A, B, C, D, E, F).

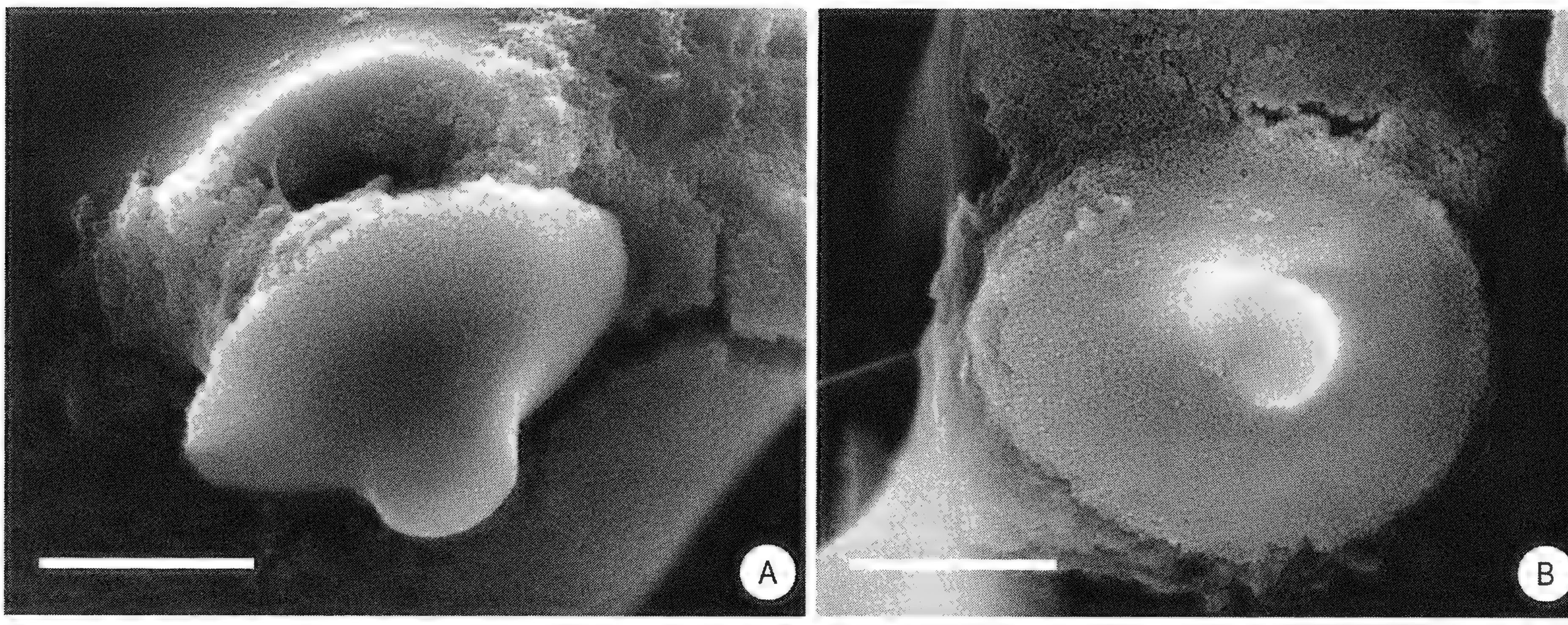

FIG. 2A-2B. Silica bodies in the form of conical projections on epidermal cells of *Selaginella conduplicata* microphylls. Bars: 2 μm.

Medial-costal (Fig. 3G–3H).—Silica bodies distributed over the microphyll intermediary region and midrib.

DISCUSSION

Terminological variation.—The occurrence of silica bodies throughout the microphyll epidermis in *Selaginella* is in accordance with the reports to *S. bryopteris* (L.) Baker (Chauhan *et al.,* 2009), *S. erythropus* (Reshak and Sheue, 2012), *S. kraussiana* (Le Coq *et al.,* 1973; Robert and Laroche, 1979; Robert *et al.,* 1973; Waterkeyn and Bienfait, 1967; Waterkeyn, Bienfait, and Peeters, 1982), *S. pallescens* (C. Presl) Spring var. *pallescens* (Dengler and Lin, 1980), and *Selaginella* sp. (Trembath-Reichert *et al.,* 2015). Based on the parameters of photographic analyses from the abovementioned publications and on the present analysis of 55 *Selaginella* representatives, the structures that have been cited in morphological descriptions of recent taxonomic studies as "idioblasts," "papillae," and "papillate idioblasts" (Góes-Neto and Salino, 2018; Góes-Neto, Heringer, and Salino, 2015; Góes-Neto, Assis, and Salino, 2017; Valdespino, 2015a,b,c; Valdespino *et al.,* 2015; Valdespino, 2017a,b; Valdespino, López, and Ceballos, 2018) are silica bodies, as revealed by the x-ray microanalysis performed in our study.

Conceptually, "idioblasts" are specialized cells that occur individually and are dispersed among vegetative and reproductive tissues, having a predominantly secretory function (Fahn, 1979; Roshchina and Roshchina, 1993), whereas "papillae" can be defined as projections of the outer periclinal wall of epidermal cells (Metcalfe and Chalk, 1979); "papillate idioblasts" would be a fusion of the two terms. Thus, considering previous reports on the structural features of silica bodies and their distribution among *Selaginella* representatives, all such terms have been employed incorrectly, and here we stress the importance of terminological standardization in further studies.

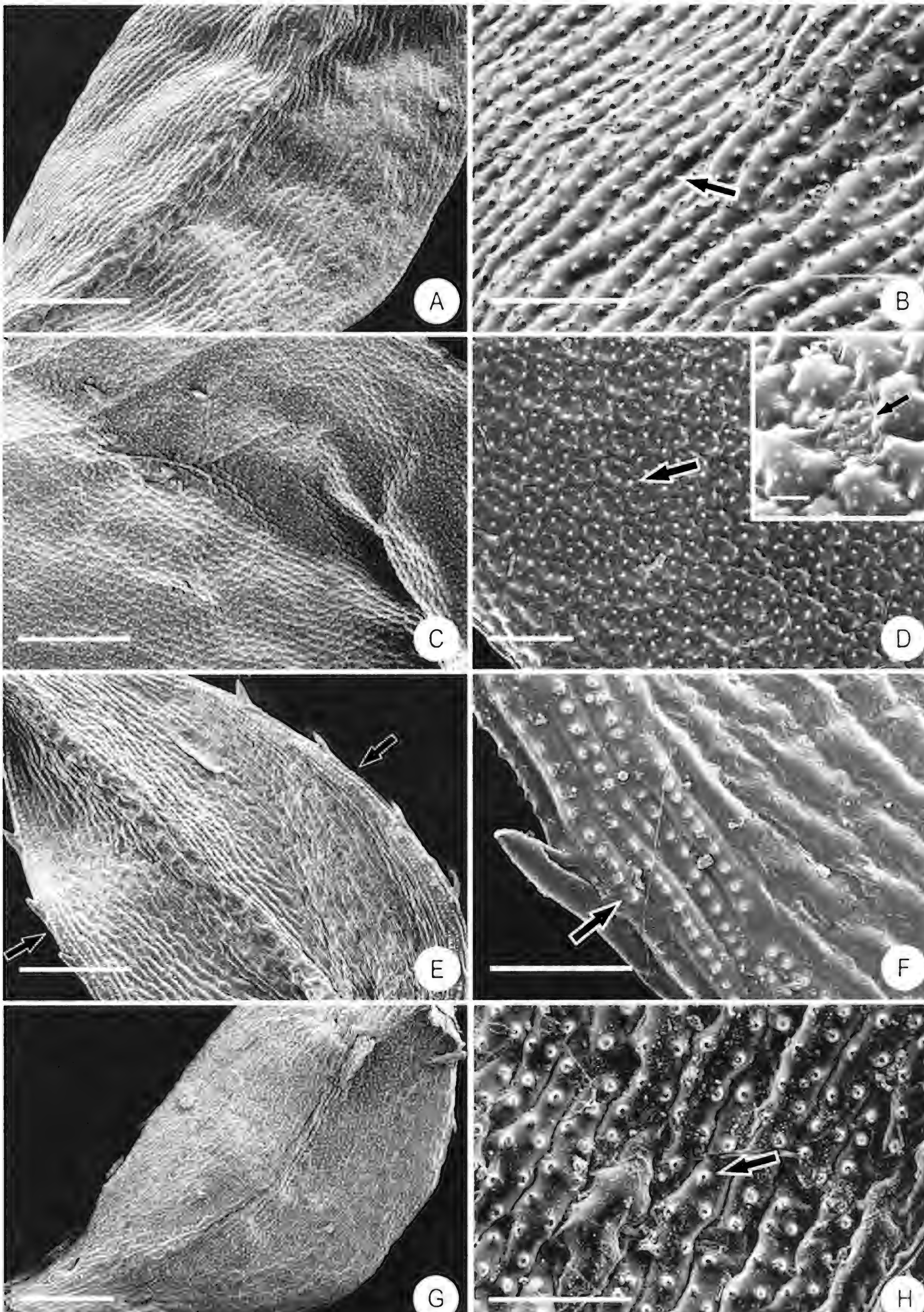

FIG. 3. Distribution patterns of silica bodies on the microphyll epidermis of *Selaginella*. **A–B**. *Selaginella marginata*, medial-marginal pattern. **C–D**. *S. minina*, laminar pattern, ***inset* D**. *S. simplex*, detail of silica bodies in greater detail. **E–F**. *S. kraussiana*, marginal pattern. **G–H**. *S. sulcata*, medial-costal pattern. Silica bodies (arrows). Bars: 10 μm (*inset* D), 20 μm (H), 50 μm (B, D, F), 200 μm (A, C, E, G).

TABLE 2. Distribution patterns of silica bodies on *Selaginella* microphylls. **Medial-marginal**, silica bodies restricted to the margin and intermediary region of the microphyll. **Laminar**, silica bodies distributed across all regions of the microphyll lamina. **Marginal**, silica bodies restricted to the leaf margin. **Medial-costal**, silica bodies distributed over microphyll intermediary region and midrib. **Absent**, silica bodies not observed in the leaf epidermis.

Taxon	Distribution patterns
***Selaginella* subg. *Exaltatae* Weststrand & Korall**	
S. anaclasta Alston ex Crabbe & Jermy	Medial-marginal
S. exaltata (Kunze) Spring	Marginal
***Selaginella* subg. *Gymnogynum* (P.Beauv.) Weststrand & Korall**	
S. asperula Spring	Medial-marginal
S. conduplicata Spring	Medial-marginal
S. epirrhizos Spring	Medial-marginal
S. fragilis A. Braun	Medial-marginal
S. geniculata (C. Presl) Spring	Medial-marginal
S. kraussiana (Kunze) A. Braun	Marginal
S. lingulata Spring	Medial-marginal
S. marginata (Humb. & Bonpl. ex Willd.) Spring	Medial-marginal
S. parviarticulata W.R. Buck	Laminar
S. parkeri (Hook. & Grev.) Spring	Medial-marginal
S. suavis (Spring) Spring	Marginal
S. sulcata (Desv. ex Poir.) Spring ex. Mart.	Medial-costal
S. silvestris Aspl.	Absent
S. tomentosa Spring	Medial-marginal
***Selaginella* subg. *Rupestrae* Weststrand & Korall**	
S. sartorii Hieron.	Medial-marginal
S. sellowii Hieron.	Medial-marginal
S. rupestris (L.) Spring	Laminar
***Selaginella* subg. *Selaginella* P. Beauv.**	
S. selaginoides (L.) P. Beauv. ex Schrank & Mart.	Absent
***Selaginella* subg. *Stachygynandrum* (P.Beauv. ex Mirb.) Baker**	
S. amazonica Spring	Medial-marginal
S. apoda (L.) Spring	Marginal
S. applanata A. Braun	Laminar
S. beitelii A.R. Smith	Absent
S. bombycina Spring	Medial-marginal
S. brevifolia Baker	Medial-marginal
S. breynii Spring	Laminar
S. coarctata Spring	Medial-marginal
S. contigua Baker	Medial-marginal
S. convoluta (Arn.) Spring	Medial-marginal
S. decomposita Spring	Medial-marginal
S. erythropus (Mart.) Spring	Medial-marginal
S. falcata (P. Beauv.) Spring	Medial-marginal
S. flagellata Spring	Medial-marginal
S. flexuosa Spring	Medial-marginal
S. homaliae A. Braun	Medial-marginal
S. kochii Hieron.	Medial-marginal
S. lechleri Hieron.	Medial-marginal
S. microdonta A.C. Sm.	Medial-marginal
S. microphylla (Kunth) Spring	Laminar

TABLE 2. Continued.

Taxon	Distribution patterns
S. minima Spring	Laminar
S. mucugensis Valdespino	Laminar
S. muscosa Spring	Medial-marginal
S. nanuzae Valdespino	Laminar
S. pallescens (C. Presl) Spring	Medial-marginal
S. potaroensis Jenman	Marginal
S. producta Baker	Medial-marginal
S. pulcherrima Liebm.	Laminar
S. radiata (Aubl.) Spring	Medial-marginal
S. revoluta Baker	Laminar
S. rhodostachya Baker	Marginal
S. seemannii Baker	Marginal
S. simplex Baker	Laminar
S. tenuissima Fée	Laminar
S. willdenowii (Desv. ex Poir.) Baker	Absent

The wide variation found in the terminology of silica bodies in the literature may be related to the scarcity of studies performed with a robust sampling and with tests for the chemical composition of mineral inclusions. This problem has been encountered over the years by specialized taxonomists and it has led to successive replication of varied terminologies, although occasionally attempts to apply those terms to silica bodies is quite understandable. The same situation has been observed in the taxonomy of Pteridaceae (Sundue, 2009), in which the use of terms such as "spicular cells," "idioblasts" and "venuloid idioblasts" resulted in the neglected systematic potential of silica bodies, which, after careful review, were shown to be a synapomorphy for the family.

Taxonomic and ecological implications.—Although silicon absorption and deposition are influenced by environmental factors, the genetic control of these two processes is the predominant factor (Piperno, 1988). Representatives of plant families that are considered non-accumulators do not accumulate silica regardless of environmental conditions. Thus, plants that present different types of silica deposition retain the individual morphologies of their inclusions when cultivated under identical environmental conditions (Prychid, Rudall, and Gregory, 2003).

The occurrence of silica bodies in four distribution patterns demonstrates the diversity with which these structures may be arranged in microphylls. The "medial-marginal" pattern was the most frequent one among the *Selaginella* species investigated in our study. Although no pattern was found to be exclusive to any subgenus, silica bodies can be considered important diagnostic characters for taxonomic studies (Prychid, Rudall, and Gregory, 2003). They have already been used to identify *Selaginella* species, despite the wrong non-specific denominations adopted, as observed in studies by Góes-Neto, Heringer, and Salino (2015), Valdespino (2015a), Góes-Neto, Assis, and

Salino (2017) and Valdespino, López, and Ceballos (2018). We expect the present terminology review to further assist future identifications of species in the *Selaginella* genus.

Concerning topology, 92% of the analyzed species have epidermal silica bodies, which may be a unifying feature for *Selaginella*, as suggested by Dengler and Lin (1980). However, further in-depth studies based on the evolution of this character in *Selaginella* remain necessary for a full understanding of their importance to the group.

When occurring on the leaf lamina, silica bodies are usually present in plant regions subjected to higher water loss (Prychid, Rudall, and Gregory, 2003). When associated with the cuticle, they regulate epidermal transpiration rate (Yoshida, Ohnishi, Kitagishi, 1962). According to Chauhan *et al.* (2011), silica bodies play a major role in reducing plant transpiration, as they act as hinges that enable the rolling of leaves under water deficit. Thus, the occurrence of silica bodies is directly related to unfavorable climatic conditions. On the other hand, weathering of silicate minerals is believed to be accelerated under wet climates, with higher amounts of soluble silica being released to the soil under those conditions than in dry climates (Dunne, 1978; Siever, 1967), which could partly explain the high silica concentrations found in species from tropical soils. In addition, although we have not proposed as a goal of our study to analyze the function of silica bodies, we highlight that the presence of silica may be related to mechanical cell-wall protection (Moraes *et al.,* 2004), activation of defense mechanisms (Ma and Yamaji, 2008), and supposedly providing support for microphylls (Dengler and Lin, 1980).

Conclusions

All previous reports that have adopted the terms "warty sclereids," "warty fibers," "epidermal warts," "papillate cells," "papillate idioblast-like cells," "elongate, papillate cells," "elongate, idioblast-like papillate cells," "idioblasts," "papillae," and "papillate idioblasts" were confirmed to refer to silica bodies. By carrying out a terminology review and establishing distribution patterns of silica bodies on the microphylls of *Selaginella*, the present research has allowed for extending the taxonomic implications of these structures to the entire genus. Further in-depth analyses based on studies of the evolution of this character remain necessary to elucidate its relevance for the ecological relationships and systematics of *Selaginella*.

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The Hybrid Fern *Polystichum* × *arendsii*

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Abstract.—The hybrid *Polystichum* × *arendsii* was first bred by Georg Arends at the turn of the 20th century. It was an artificial cross between *P. munitum* (Kaulf.) C. Presl, native to north western North America, and *P. aculeatum* (L.) Roth, occurring in the Eurasian region. In 1906 the well-known Swiss botanist Konrad H. Christ applied the name *Aspidium* × *arendsii* to this hybrid. In the following decades the fern was lost and its name was forgotten. The present study investigates the history of the hybrid. In the interim, the cross has been successfully carried out once again and a new description of *P.* × *arendsii* is provided. Study of herbarium material and comparison of the information supplied by Konrad H. Christ, as well as the analysis of the spores, confirmed that the hybrid corresponds with the original *A.* × *arendsii* and a necessary valid combination under *Polystichum* is provided.

Key Words.—Arends; Hybrid; *P. munitum; P. aculeatum*; comb. nov.

Georg Arends (1863–1952) was a German horticulturist and plant breeder whose historic nursery of perennials is located in the Ronsdorf area of Wuppertal. Of the 300 perennials he bred throughout his life, he left a detailed record of the creation of one: a fern hybrid subsequently referred to as *Aspidium arendsii* F.Wirt. ex Christ. He prepared this hybrid by sowing a mixture of spores from *A. lobatum* (Huds.) Sw., now known as *P. aculeatum* (L.) Roth, and *A. munitum* Kaulf., now known as *P. munitum* (Kaulf.) C. Presl. The resulting mixture of gametophytes permitted cross fertilization, and the hybrid between the two species developed. (Arends, 1951)

Around 1905, Arends supplied a correspondent, August Hahne, and others with material of the hybrid; Hahne, in turn, passed it to the taxonomist Ferdinand Wirtgen. Konrad H. Christ learned of *A. arendsii* through Wirtgen and published a description of the hybrid in 1906, validating the name and favorably appraising its horticultural prospects (Christ, 1906). In subsequent decades, the hybrid was lost (Arends, 1951) and its name forgotten. Anne Sleep described the successful cross-breeding of *P. aculeatum* × *munitum* during her studies on the cytology of *Polystichum* (Sleep, 1966), but the name *A.* × *arendsii* was not mentioned. Rolf Thiemann regenerated the hybrid in approximately 1999, and described the result under the name *Polystichum* × *arendsii* (Thiemann, 2013). However, his citation of A. *arendsii* lacked the page number required by a "full and direct reference" under the International Code of Nomenclature.

Since 2008, the "Georg Arends Förderkreis e.V." (GAF) has sought to preserve Arends' horticultural and cultural heritage. A significant part of the GAF's activities involves cultivating and preserving Arends' perennials in a so-called living plant archive. As an experienced gardener and long-time fern

expert and as an active member of the GAF, I have sought to find extant specimens of ferns bred by Arends, and to re-breed the hybrid named for him.

The existence of this hybrid is of greater scientific interest than simply the commemoration of Arends, however. The disjunction between the natural ranges of the parents, *P. munitum* in the Pacific Northwest of North America and *P. aculeatum* in Europe, would normally prevent their hybridization outside of a laboratory. *Polystichum munitum* has, however, become naturalized in England, and its hybrid with the native *P. setiferum* (Forssk.) T.Moore ex Woynar, *P.* × *lesliei* Rumsey & Acock, has been found in the wild. (Acock *et al.*, 2011) Natural hybrids with native *P. aculeatum* might also be expected to occur where their ranges now overlap. To facilitate their recognition, I provide a detailed description of the hybrid's morphology, and validate the combination *P.* × *arendsii*.

Materials and Methods

Crossing experiments.—The re-breeding of the hybrid was carried out with single specimens of *P. munitum* and with *P. aculeatum* sporophytes, from Georg Arends' own collections. These were examined morphologically to confirm their determination. Freshly collected spores from the parent plants were sown in separate containers. The hybridization steps involved followed those of Piller (2014) and the work was carried out under horticultural conditions with growth substrate (a commercially available mixture of peat with added sand and clay). After approximately four months cultivation in a small greenhouse (temperature maintained at 22–24 °C, under aseptic conditions) numerous prothallia of both species developed. Forty prothallia of the two species were paired and planted close together to favor crossing. This resulted in the growth of three hybrid sporophytes of *P. aculeatum* × *P. munitum*. Of the three individuals obtained, one is currently growing in the personal collection of the author and two in the historic nursery of the "Anja Maubach – Arends Staudengärtnerei" in Wuppertal-Ronsdorf.

Authentication.—The authenticity of *P.* × *arendsii* was confirmed in two steps: First, examination of the spores and their photographic documentation revealed the hybrid character of the individuals, with aborted spores and a few diplospores (Fig. 1). Second, comparison with a specimen of Arends' material collected in 1905 (B 20 0142640), hereafter designated as type, with the re-bred original, revealed no morphological differences, apart from the age of the specimen.

Results

Description of *Polystichum* × *arendsii*

The following morphological description of *P.* × *arendsii* is based on the specimen B 20 0142640 and on the re-bred hybrid grown in the "Georg Arends Staudengärtnerei" in Wuppertal, Germany.

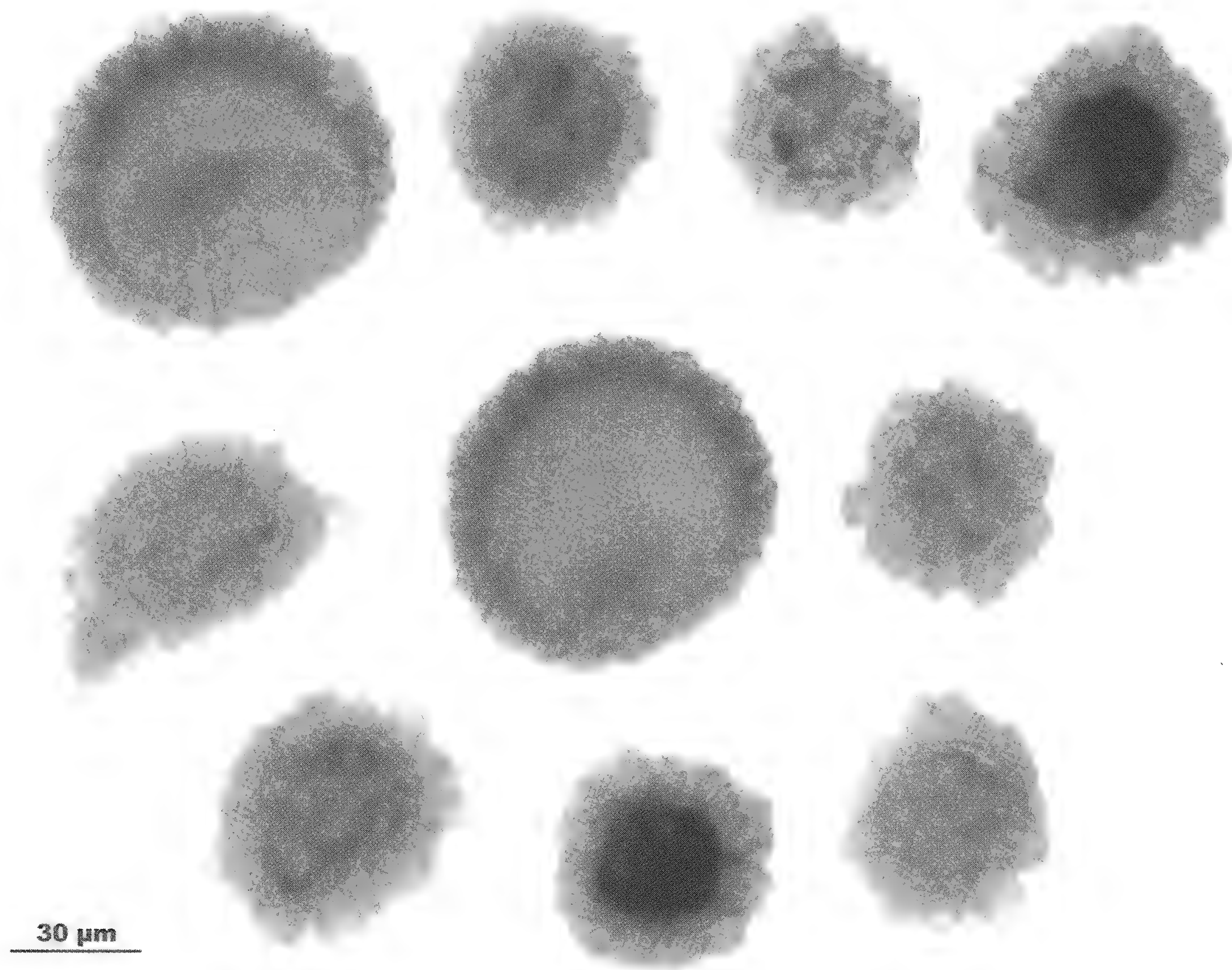

FIG. 1. Viable and aborted spores of *P.* × *arendsii* (Photo by Dr. Ralf Wagner, Düsseldorf)

Growth habit.—Initially funnel-shaped and erect, later strongly arcuate, overhanging leaves. Total height therefore only about 60% of the length of the leaves (Fig. 2).

Rhizome.—Short, erect, densely covered with brown scales.

Leaves.—Arrangement rosette-like, later re-growing out of the centre, about ≥ 100 cm long and 18 cm wide, surface leathery, overwintering.

Petiole.—Length 5–15% of leaf length, to 7 mm thick, ventrally slightly grooved, brown at the base, becoming light green apically, densely set with irregularly-sized scales, 5 vascular bundles present in the base, gradually uniting apically.

Scales.—Nut brown, lighter at the margins, ovate-lanceolate at the stipe base, ending in an aristate tip, about 10 mm in size, becoming smaller and frayed apically.

Lamina.—About 90 cm long, lanceolate to linear-lanceolate, long-pointed, significantly narrowed at the base, bi-pinnate basally, pinnate apically; dorsally dark green, dull-glossy to dull, glabrous; ventrally pale, slightly lighter grayish-green; set with small light brown scales.

Rachis.—Scaly, grooved, bright green, paler apically.

FIG. 2. Habit of two-year-old *P.* × *arendsii*, 05.06.2012 (Photo by S. Piller)

Pinnae.—Opposite, alternate medially; median pinnae 8–10 cm long, linear-lanceolate, often bent apically, curved or S-shaped, pinnatisect to pinnatifid in the basal portion, the apical half to third serrate, apex spinulose (Figs. 3 and 4).

Pinnules.—Alternating, slightly to exauriculate, closely together, becoming in the second half or in the last third towards the tip of the pinna merging to pinnatifid, variations possible, all ending in an aristate tip, ventrally distinctively veined (Figs. 3 and 4).

Upper pinnules.—Rhombic oval-ovate, very short-petiolulate or adnate to the costa, margins irregularly spiny, about 10 mm long; the first acroscopic pinnules at pinna base larger, about 15 mm long, slightly to exauriculate, laterally converged to the rachis (Figs. 3 and 4).

Lower pinnules.—One-third shorter than the upper ones, somewhat rhombic, exauriculate, short-petiolulate at base, above sessile, otherwise like the upper ones (Figs. 3 and 4).

Sori.—In the upper 2/3 to 3/4 part of the blade on the abaxial surface of the pinnules in double rows on the veins, one to seven sori per pinnule at the pinna apex often merging, up to 14 near the base, 0.5–1.0 mm in size, indusium approximately round of same size (Fig. 4).

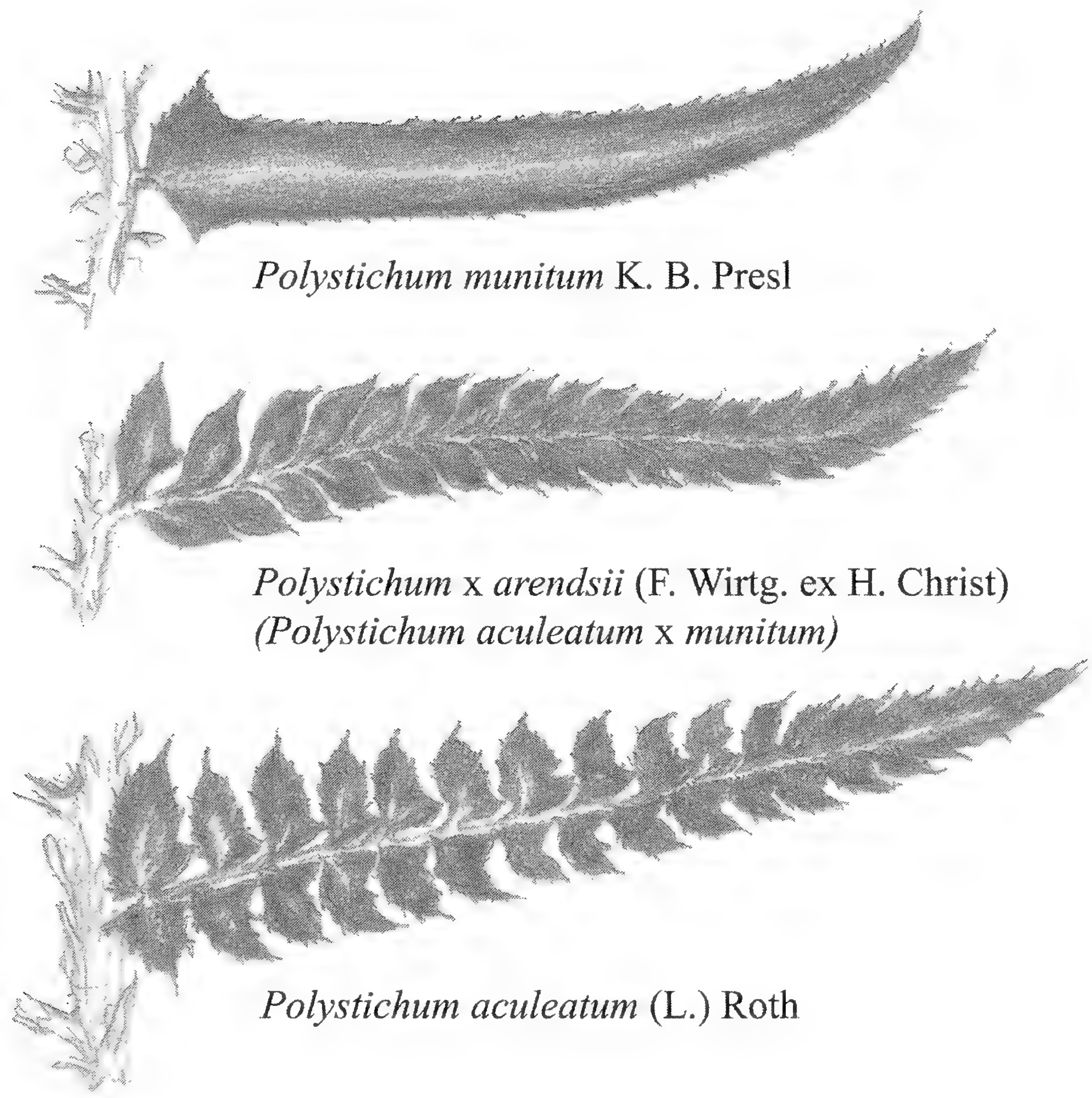

FIG. 3. Comparison of pinnae and pinnules of *P. munitum*, *P.* × *arendsii*, and *P. aculeatum* (Drawing by S. Piller)

FIG. 4. Pinnae of *P.* × *arendsii*, left: lower surface, with sori, adult; right: upper surface, juvenile (Photo by S. Piller)

TABLE 1. Comparative morphology of the hybrid *Polystichum* × *arendsii* and both parent plants.

	P. munitum (Kaulf.) C. Presl	*P.* × *arendsii* (F. Wirtg. ex Christ)	*P. aculeatum* (L.) Roth
Growth habit	Slender, funnel-shaped overhanging leaves, about 80 cm long.	Initially funnel-shaped and erect, later strongly arcuate overhanging, spiraling leaves. about 100 cm long,	Broad, funnel-shaped overhanging leaves, about 90 cm long.
Lamina	About 65 cm long and 16 cm wide, strictly linear-lanceolate, slightly narrowed at the base, singly pinnate; dorsally dark green, dull; ventrally medium green.	About 90 cm long and 18 cm wide, lanceolate to linear-lanceolate, long pointed, significantly narrowed at the base, doubly pinnate basally, singly pinnate apically; dorsally dark green, dull-glossy to dull, glabrous; ventrally pale, slightly lighter grayish-green; set with small light brown scales.	About 75 cm long and 22 cm wide, lanceolate, narrowed at the base, doubly pinnate; dorsally dark green, glossy; ventrally gray-green; set with brown scales.
Pinnae (Fig. 3)	Up to 8 cm long, slender linear-lanceolate, rarely bent apically, clearly serrate, basally strongly auriculate, apex spinulose.	Median pinnae 8–10 cm long, linear-lanceolate, often bent apically, curved or S-shaped, pinnatisect to pinnatifid in the basal portion, the apical half to third serrate, apex spinulose.	Up to 11 cm long, lanceolate, straight, apically pointed, pinnate.
Pinnules (Fig. 3)	Non-existent	slightly to exauriculate, closely together, becoming in the second half or in the last third towards the tip of the pinna merging to pinnatifid.	Basally strongly auriculate, apart from each other, hairy.
Upper Pinnules (Fig. 3)	Non-existent	Rhombic oval-ovate, non-auriculate, very short-petiolulate or adnate to the costa, margins irregularly spiny, about 10 mm long; the first acroscopic pinnules at pinna base larger, about 15 mm long.	Lanceolate-ovate, basally auriculate, short-petiolulate, margins spiny, about 12 mm long; the first acroscopic pinnules at pinna base about 20 mm long, auriculate.
Lower Pinnules (Fig. 3)	Non-existent	One-third shorter than the upper pinnules, exauriculate, short-petiolulate at base, above sessile, first pinnate laterally converged to the rachis.	Slightly shorter than the upper pinnules, basally slightly auriculate, petiolulate, first pinnate protruding from the rachis.

Spores.—Mostly aborted, misshapen, a few larger, approximately spherical (possibly diploid), perispore dense with short, foliolate or hairlike curved extension (Fig. 1).

The hybrid *P.* × *arendsii* is compared to its parents in Table I. The hybrid plant is morphologically similar to *P. aculeatum*. However, it differs from this species in that it has longer and narrower leaves, shorter and linear-lanceolate pinnae as well as smaller, rhombic oval-ovate pinnae which are not eared and are sparsely hirsute. *Polystichum* × *arendsii* is distinguished from *P. munitum* by its distinct, bipinnate leaves and its upright funnel-shaped habit. The color of the leaves is intermediate between the two parent species. The sori are approximately equal to those of *P. aculeatum*. Less than 0.1 % of the spores of *Polystichum* × *arendsii* are viable.

Discussion

The hybrid *P.* × *arendsii* has been successfully re-bred and has been proven to be identical with the original material. It may be sought as a spontaneous hybrid in areas where *P. munitum* has naturalized in the vicinity of *P. aculeatum*.

A formal combination follows:

Polystichum × *arendsii* (F. Wirtg. ex Christ) R. Thiemann ex S. Piller, **comb. nov.** Basionym: *Aspidium arendsii* F. Wirtg. ex Christ, Allg. Bot. Z. Syst. 12:4. 1906. TYPE: Ronsdorf (b. Elberfeld), comm. *F. Wirtgen s.n.*, Oct. 1905 (lectotype, designated here, B 20 0142640 [digital image!]).

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COVER CAPTION: Two-year old *Polystichum* × *arendsii*. Photo credit: S. Piller